COGNITION, EVOLUTION, AND BEHAVIOR

SECOND EDITION

Sara J. Shettleworth

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Second Edition

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Preface

What this book is about

The study of the animal mind is one of the most exciting areas in the cognitive sciences. The feats of navigation performed by bees and pigeons, tales of talking parrots and counting rats, self-aware chimpanzees and tool-using crows not only fascinate the nonspecialist, they raise important issues in psychology and biology. How do bees or pigeons find their way home? Can other animals navigate as well as they do, and if not, why not? Do parrots really talk? What use would counting be to rats in the wild anyway? Do monkeys and apes, which look so much like us, think like us too? What is the relationship between the human mind and the minds of other species?

Questions like these raise issues that are intrinsically interdisciplinary. Because of this they have traditionally been covered inadequately in most textbooks, although they are often the subject of popular and semipopular treatments. Introductions to animal cognition for psychology students have usually reviewed laboratory studies of rats, pigeons, and monkeys from an anthropocentric point of view. Evolutionary issues or observations of behavior outside the laboratory have typically been oversimplified or not discussed at all. On the other hand, introductions to animal behavior or behavioral ecology include at most a brief survey of research on animal learning and cognition, even though the authors may point out that the sorts of cognitive processes generally studied by psychologists play a role in ecologically relevant behavior. A zoologist wishing to know more soon feels mired in the psychologist's specialist terminology. Equally specialized terms await the psychology student wanting to know more about evolution and behavioral ecology. Phylogeny, MVT, and ESS are just as baffling to the uninitiated as US, RI, and fixed interval schedule.

I wrote the first edition of this book in the belief that the future of research on comparative cognition, behavioral ecology, and behavioral neuroscience lies in increased interdisciplinary training and communication. I tried to capture a vision of an approach to the evolution of the mind in which it is natural, indeed necessary, to integrate the answers to questions traditionally asked in psychology laboratories with the answers to questions about ecology and evolution. I tried to make it accessible to students and researchers from both psychology and biology, or with backgrounds in neither. It was for the increasing numbers of people trained in the cognitive sciences who are finding that their discipline must embrace consideration of species other than humans and that the study of cognition in any species is incomplete without consideration of evolution and ecology.

Equally, it was for behavioral ecologists and ethologists who find themselves wanting to answer essentially psychological questions about behavior.

Why a second edition?

The decade since the first edition of *Cognition, Evolution, and Behavior* was written has seen an explosion of new developments in almost every area it covers. Many of them are around the boundary that traditionally divided comparative psychology from the biological study of behavior, the very boundary that *Cognition, Evolution, and Behavior* focused on bridging. There is now every sign that a truly integrative cross-disciplinary research program on comparative cognition has finally taken off. As a happy result, many parts of the first edition are outdated. This second edition integrates new developments and insights with earlier material. To mention a few examples, associative learning has seen new challenges to what has been the dominant theory in the area for almost a half century. New studies of whether animals are aware of their memories or have "episodic like" memory—questions hardly touched by serious researchers before 1998—raise fundamental issues about the promises and limits of what we can learn from comparing verbal and nonverbal species. Comparative studies of numerical cognition, spatial cognition, and animal communication have taken important new directions and seen more theoretical integration with work on child development and with neuroscience. The study of social learning and animal culture has exploded. Analyses of social cognition in field and laboratory, including the contentious topic of whether other species have theory of mind, have been extended to species as diverse as dogs, hyenas, goats, ravens, and fish. Spirited debates about whether any animals can be said to teach their conspecifics or to have culture have been fueled by prominent new discoveries, not only with primates but with other species. Likewise, studies of tool using—both fieldwork documenting its occurrence and analyses of what tool-users know—now include birds as well as a range of primates. As with studies of social cognition, the possibility of convergence in evolutionarily diverse species promises important insights into the conditions for evolution of human-like behavior and understanding. We are seeing the development of a much more detailed, nuanced, and biologically informed view of how and why species are both the same and different cognitively, including of course what humans share with other species and how we may be unique.

How this book is organized

Like the first edition of *Cognition, Evolution, and Behavior,* this one aims to be a comprehensive cross-disciplinary account of contemporary research on animal cognition in the broadest sense, from perception to the bases of culture, and to be accessible to students and specialists alike. The general approach and organization are the same as for the first, but with 15 rather than 13 chapters. The old Chapter 1 is divided into two to permit explicit discussion of classic foundational issues such as the role of Morgan's Canon that are so clearly still at stake today. New discussions of the relationship between brain evolution and cognition justify a separate Chapter 2 for background on evolution and on the brain that was originally part of Chapter 1. As before, the order of subsequent substantive chapters implies a "bottom-up" approach to cognition, starting with perception and simple forms of learning along with some basic concepts from ethology and building up to so-called higher or more complex processes. The central chapters (Chapters 3–14) are now divided into three sections, each with a short introductory overview: "Fundamental Mechanisms" (perception, learning, categorization, memory), "Physical Cognition" (space, time, number, physical causation), and "Social Cognition" (social knowledge, social learning, communication).

One major change is the placement of timing and counting in separate chapters, recognizing how new research and theorizing have transformed the study of numerical cognition into a key area of comparative research in its own right. At the same time, material on subjects where there have been few new developments has been condensed. For example, optimal foraging is now part of a comprehensive treatment of instrumental behavior that also includes economic decision-making, tool use, and planning. In another reorganization, the three chapters on aspects of social cognition now begin with a chapter on the nature of social knowledge. This draws on the depth and breadth of new information about social understanding in wild animals from baboons to birds to provide a background for burgeoning laboratory research on social cognition and cooperation.

As in the first edition, the final chapter (here Chapter 15) reflects on what the preceding chapters teach us about some overarching issues. Here these include what comparative studies reveal about "the modularity of mind" and whether comparative cognition research can be said to have any single well-defined set of methods or theoretical approach. This chapter also looks at new contributions to what has arguably been the central discussion in comparative studies of the mind since their beginnings in the late 19th century: how are humans different from other species, and why? In the concluding chapter of *The Origin of Species* Darwin (1859) prophesied, "In the future I see open fields for far more important researches. Psychology will be securely based on the foundation . . . of the necessary acquirement of each mental power and capacity by gradation. Much light will be thrown on the origin of man and his history." He would no doubt be pleased to see that, along with all the other amazing fields opened up by his insights, this one is yielding such a rich harvest.

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Acknowledgments

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For practical matters, I thank Alissa Bello for help with the references, and especially Caroline Strang for so cheerfully and efficiently doing so many editorial tasks, among them obtaining all the permissions to reproduce previously published material. I am grateful to NSERC for continued support, the University of Toronto library system for instant access to everything a modern scholar could wish for, and the folks at End Note for kindly updating the formatting of the first edition. Most of all, thanks to Catharine Carlin at Oxford for her unfailing support and enthusiasm and to Dr. Margaret C. Nelson, a true collaborator without whose splendid illustrations neither the first edition nor this one would be nearly so attractive or useful. Once again, the book is dedicated to past and future students of animal cognition, especially all the students and postdocs in my lab from whom I have learned so much over the years.

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Toronto, Ontario, Canada

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Cognition, Evolution, and Behavior

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Cognition and the Study of Behavior

Walnut trees shade the streets of Davis, California. They also provide food for the crows that roost near Davis. Crows crack walnuts by dropping them from heights of 5–10 meters or more onto sidewalks, roads, and parking lots. Occasionally they drop walnuts in front of approaching cars, as if using the cars to crush the nuts for them. Do crows intentionally use cars as nutcrackers? Some of the citizens of Davis, as well as some professional biologists (Maple 1974, in Cristol et al. 1997) were convinced that they do, at least until a team of young biologists at UC Davis put this anecdote to the test (Cristol et al. 1997). They reasoned that if crows were using cars as tools, the birds would be more likely to drop nuts onto the road when cars were coming than when the road was empty. Furthermore, if a crow was standing in the road with an uncracked walnut as a car approached, it should leave the nut in the road to be crushed rather than carry it away.

Cristol and his collaborators watched crows feeding on walnuts and recorded how likely the birds were to leave an uncracked walnut in the road when cars were approaching and when the road was empty. They found no support for the notion that crows were using automobiles as nutcrackers (Figure 1.1). In other respects, however, the birds' behavior with walnuts was quite sophisticated (Cristol and Switzer 1999). For example, by dropping nuts from buildings on the Davis campus, Cristol and Switzer verified that English walnuts did not have to be carried so high before breaking as the harder black walnuts and that they broke more easily when dropped onto pavement than onto soil. The crows' behavior reflected these facts (Figure 1.1). A crow dropping a nut also took into account the likelihood that a greedy fellow crow might steal a dropped nut before it could be retrieved: the fewer crows waiting on the ground nearby, the higher they took walnuts before dropping them.

The story of the nutcracking crows encapsulates some key issues in the study of cognition in animals. Foremost is how to translate a hypothesis about essentially unobservable internal processes into hypotheses about behavior in a way that permits different explanations to be distinguished. Here, this meant asking, "What will crows do if they are using cars as tools that they will not do if they are merely dropping nuts onto the road as a car happens by?" A second issue has to do with the kinds of hypotheses people entertain about the processes underlying animal behavior. The people in Davis and elsewhere (Nihei 1995; Caffrey 2001) who saw nutcracking as an expression of clever crows' ability to reason and plan were engaging in an

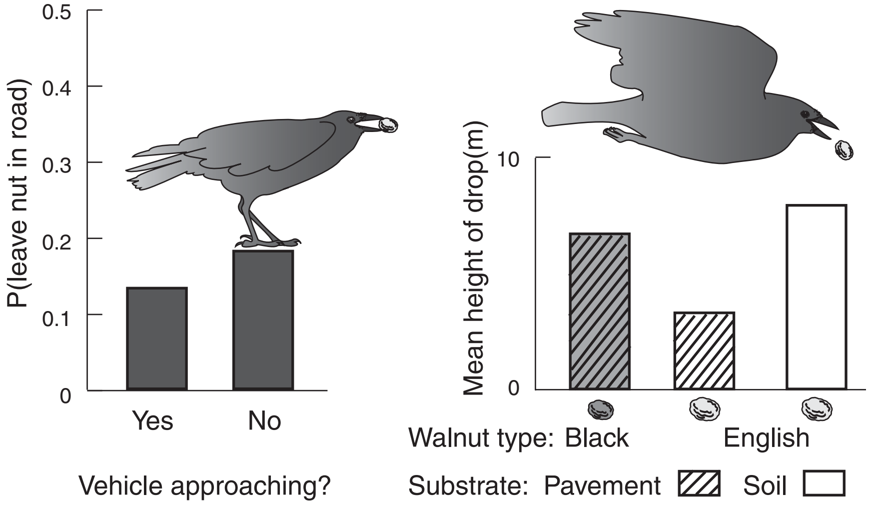

Figure 1.1. Left: Proportion of crows dropping a walnut in the road when flying away as a function of whether or not a vehicle was approaching (data from Cristol et al. 1997). Right: Mean height to which crows carried black or English walnuts before dropping them onto pavement (cross-hatched bars) or onto soil (English walnuts only) (data from Cristol and Switzer 1999).

anthropomorphism that is common even among professional students of animal behavior (see below, Section 1.3.2; Kennedy 1992; Wynne 2007a, 2007b). As we will see, such thinking can be a fertile source of ideas, but research often reveals that simple processes apparently quite unlike explicit reasoning are doing surprisingly complex jobs. Free-living crows were observed doing something suggestive of interesting information processing and decision making. Their behavior was then examined with more systematic observations and experiments. Among other things, these revealed how closely the crows' behavior matched environmental requirements. Numerous cognitive processes underlie the crows' nutcracking, and each of these could be analyzed further. For example, how do crows judge the height from which they drop nuts? Do they have to learn to adjust their behavior to the kind of nut, the kind of substrate, and the number of nearby crows? Several species of crows, gulls, and other birds break hard-shelled prey by dropping them (Cristol and Switzer 1999), and one might also ask what ecological conditions or evolutionary history favor this behavior.

1.1 What is comparative cognition about?

1.1.1 What is cognition?

Cognition refers to the mechanisms by which animals acquire, process, store, and act on information from the environment. These include perception, learning, memory, and decision-making. The study of comparative cognition is therefore concerned with how animals process information, starting with how information is acquired by the senses. The behavior examined for evidence of cognition need not be learned, and it need not be studied in the laboratory by psychologists. In this book how birds classify songs in the field will be considered alongside how animals can be taught to classify artificial stimuli in the laboratory (Chapter 6). Possible natural examples of tool use like the crows' nutcracking will be examined along with tests of what captive animals understand when they use tools (Chapter 11). The dance communication of bees and the alarm calling of chickens will be considered alongside the use of human gestures, words, and symbols by parrots and chimpanzees (Chapter 14). How ants find their way in the desert and how rats find their way in mazes will both be examined for what they reveal about the principles of spatial cognition (Chapter 8).

Not all agree that such an inclusive definition of cognition is useful. *Cognitive* is often reserved for the manipulation of declarative rather than procedural knowledge (e.g., Dickinson 2008). Declarative knowledge is "knowing that" whereas procedural knowledge is "knowing how," or knowing what to do. The declarative knowledge that a chipmunk might gain from moving about its territory could be maplike: "Home burrow is south of that big rock." Or the chipmunk might store information about its territory as procedural knowledge such as "Turn left at the rock." The first kind of representation implies more flexible behavior than the second, but in both cases behavior results from processing and storing information about the world. A related distinction is that between first-order and higher-order processes, only the latter of which may be regarded as interestingly cognitive. First-order processes operate directly on perceptual input, as when a stimulus triggers a response or creates a trace in memory. Second-order processes operate on first-order processes, as in evaluating the strength of one's memory for an event (Heyes 2008; Penn, Holyoak, and Povinelli 2008).

For many psychologists, mental representations of the world or computations on them are the essence of cognition. However, it is almost never possible to tell without experimental analysis what kinds of processes are reflected in a given behavior. Moreover, functionally similar behavior, such as communicating, recognizing neighbors, or way finding, may be accomplished in different ways by different kinds of animals (Dyer 1994). Much interesting adaptive behavior results from processing limited information in simple ways, and the richness of the representations underlying behavior varies considerably across species and behavior systems. Because comparing the ways in which different species solve similar information-processing problems is an important part of the comparative study of cognition, it should embrace all sorts of information processing and decision-making.

1.1.2 *Animal* cognition or *comparative* cognition?

Referring to the field of research discussed in this book as *comparative* rather than *animal* cognition is similarly inclusive. Some classic assessments of psychological research on animals (Beach 1950; Hodos and Campbell 1969; Dewsbury 1998) are complaints that most studies labeled "comparative" are mere "animal psychology" because they deal with only a single nonhuman species or at most implicitly compare that one species with humans. As we will see, the situation in the early twenty-first century is dramatically different. More species are being studied and compared with one another, and findings are interpreted with increasing biological sophistication. But there is still a good deal of research aimed at analyzing particular processes in depth in one or a few species. It is especially prominent in the section of this book on Basic Processes (Chapters 3–7). But thorough analyses of cognitive processes in limited species form the foundation for comparative work, as when comparisons of memory in food storing and nonstoring birds (Chapters 2 and 7) draw on method and theory developed in studies with pigeons. Therefore "animal cognition" research is part of the overarching enterprise referred to in this book as research on comparative cognition aimed at understanding cognition across the animal kingdom, including how it works, what it is good for in nature, and how it evolved.

1.1.3 Consciousness and animal cognition

People intuitively distinguish between merely responding to events and being aware of them, as when someone driving along a busy highway while deep in conversation says, "I wasn't conscious of the passing miles." Perceptual awareness can be distinguished from reflective consciousness, which might be evidenced when the driver mentally compares possible routes to her destination, perhaps evaluating her own ability to recall their details (self-reflective consciousness).

Within psychology, the rise of behaviorism in the early 1900s threw introspective studies of consciousness into disrepute. The cognitive revolution of the 1960s and 1970s continued this tradition. Studying cognition meant inferring how information is processed from analyzing input-output relations without regard for the extent or kind of concomitant awareness. But in the last decade or so of the twentieth century, the study of consciousness in humans and other species became not only scientifically respectable but an active area of research. One impetus for this work was the discovery of striking phenomena such as "blindsight" (Box 1.1) and priming in memory (Chapter 7), which reveal distinct conscious and unconscious processes in

Box 1.1 Vision with and without Awareness

Neurological patients with "blindsight" react to objects in the visual field without reporting awareness of them (Weiskrantz 1986). If such patients, who have damage in area V1 of the visual cortex, are shown an object in the affected part of the visual field, they report seeing nothing. However, when they are forced to point to the object's location or guess its characteristics, they perform above chance. Thus these people seem to have vision without awareness. Visual detection apparently can be dissociated from visual awareness in monkeys, too (Cowey and Stoerig 1995, 1997). Three monkeys with lesions to area V1 were trained in two different tasks (Figure B1.1). One was analogous to asking them "Do you see it?" and the other, to asking them "Where is it?" The lesions affected only the right half of each monkey's visual field, so each monkey's performance to stimuli there could be compared to its performance when stimuli were shown in the field with normal vision. To control the part of the retina stimulated, displays were presented briefly while the monkey was fixating a spot in the middle of a computer screen.

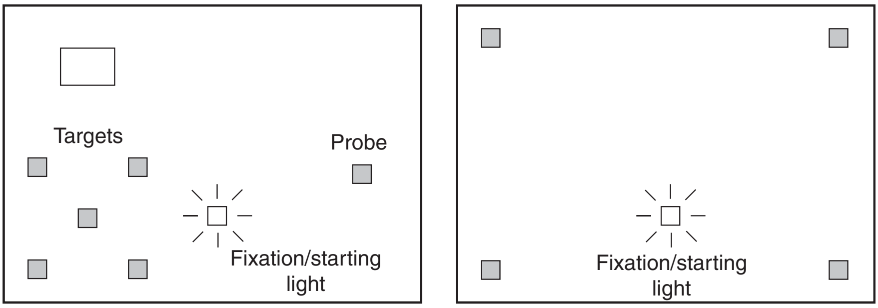

Figure B1.1. Stimulus displays for testing blindsight in monkeys. Redrawn from Cowey and Stoerig (1995) with permission.

To train the monkeys to report “I see it,” a stimulus was presented any of five positions in the lower part of the normal field, and on some trials no stimulus was presented (Figure B1.1, left). In the former case, the monkey was rewarded for touching the location where the stimulus had appeared. In the latter, it was rewarded for reporting “no” by touching a white rectangle at the top of the screen. When the monkeys were reporting presence/absence correctly on about 95% of the trials, they were tested with occasional probes in the “blind” half of the visual field. They reported “no stimulus” about 95% of the time. Importantly, a normal control monkey did transfer correct responding to this novel location. In the other task, a brief flash appeared in one of the four corners of the screen on every trial (Figure B1.1, right). The monkeys had simply to touch the location where it had appeared, in effect reporting where they saw it. In this task, performance was highly accurate for both the normal and the “blind” visual field. These data are consistent with other evidence that primates have separate visual pathways for perception and action (Goodale and Milner 1992). Like people with comparable brain damage, the monkeys appear to have vision without awareness in the affected part of the visual field, suggesting that their normal vision is accompanied by awareness.

In this example, nonverbal responses that the monkeys were trained to make substituted directly for humans’ verbal reports (“I see it,” etc.). When people with blindsight took the same nonverbal tests as the monkeys, their responses paralleled their verbal reports of awareness (Stoerig, Zontanou and Cowey 2002).

everyday cognition. Debates about the extent to which people are aware of their own cognition (metacognition; Chapter 7) have also placed a new emphasis on how subjects consciously experience their memories, percepts, or the like as distinct from how they act on them. Progress in analyzing the neural basis of behavior in such experiments through brain imaging and studies of cognitively impaired people have encouraged attempts to investigate the same processes in animals (e.g., Terrace & Metcalfe 2005). If some pattern of brain activity turns out to be necessary and sufficient for verbal reports of conscious awareness, thinking, remembering, or the like, what does it mean if this same pattern can be identified in an animal?

A central methodological problem here is that because evidence for consciousness in humans generally consists of what people say about their mental experiences, seeking it in nonverbal species requires us to accept some piece of the animal’s behavior as equivalent to a person’s verbal report. For example, in the experiment described in Box 1.1, we must accept that the monkeys’ “I see it” response indexes a subjective state equivalent to a person’s experience of seeing. Clearly we can never know whether this is correct or not, since we can never know the animal’s private state. Therefore, the point of view of most researchers studying animal cognition is that how animals process information can, and should, be analyzed without making any assumptions about what their private experiences are like. That is, the best we can do is to seek *functional similarities* between behaviors taken as evidence for given processes in humans and behaviors of animals (Staddon 2000; Hampton 2005; Heyes 2008). This approach takes support from evidence that people act without being aware of the reasons for their actions, that is, without using reflective consciousness, more often than is commonly realized. We may, for example reach for the reddest tomato on the bush and only later explain why (Carruthers 2005). A related view (Macphail 1998) is that human babies nor nonhuman animals can have reflective consciousness because it requires language.

The view that consciousness in animals is not a subject for research either because it is inaccessible to scientific study or because animals lack language was emphatically rejected by scientists calling themselves cognitive ethologists (Ristau 1991a). Stimulated by the writings of the distinguished biologist Donald Griffin (1976, 2001), cognitive ethologists claim that much behavior suggests that animals have conscious intentions, beliefs, and self-awareness, and that they consciously think about alternative courses of action and make plans (Griffin and Speck 2004). Studies of animals communicating, using tools, and apparently deceiving one another figure prominently in these discussions because they seem to reveal flexible behaviors governed by intentions to achieve specific goals. However, it is difficult to find a situation for which the notion that an animal has a conscious belief or intention or is consciously manipulating information unambiguously predicts what it does (Dawkins 1993; but see Griffin 2001). Nevertheless, the early years of the twenty-first century have seen an upsurge of provocative and sometimes controversial research addressed to exactly these issues.

Of course, some anthropomorphic mentalistic terms have traditionally been accepted to refer to processes underlying animal behavior. For example, training a rat that a tone predicts a shock is usually referred to as fear conditioning. The rat is said to fear the tone, and indeed it may be in the same physiological state as a person describing himself as fearful. Similarly, a hungry rat trained to press a lever for food could be said to be doing so because it desires food and believes that lever pressing will give it food. On one view (Chapter 11 and Dickinson 2008) the goal-directedness of bar pressing or other instrumental responding, that is, evidence that it is controlled by belief and desire, is what is meant by its being under cognitive control. Belief, desire, fear, or other mental or emotional states may be ascribed to animals on the basis of well-defined behavioral criteria, that is, on the basis of functional similarity, without implying that the animals are undergoing humanlike conscious experiences.

Thinking about how consciousness might have evolved is not much help here. On the one hand, if we accept that human beings are conscious it seems that some other species, perhaps among primates, must share at least perceptual awareness with humans (see Terrace and Metcalfe 2005). Saying that only humans are conscious in any way seems like rejecting evolutionary continuity (but see Penn, Holyoak, and Povinelli 2008). On the other hand, because evolution has acted via the results of what creatures do, not directly on what they experience privately while doing it, it seems there must be something promoting survival and reproduction that a conscious animal can do and one lacking consciousness cannot, but so far there are no clear candidates for that "something" (Dawkins 1993, 2006). This same problem of an apparent evolutionary gap between humans and other living species arises in discussions of the evolution of human language and abstract conceptual abilities (Chapter 15 and Penn, Holyoak, and Povinelli 2008). Despite the apparent successes of teaching aspects of language to apes, most would now conclude that language is unique to humans, and the conditions under which it could evolve are an active area of debate (Chapter 14). Anthropological studies of human evolution and of primate behavior in the wild are likely to add fuel to these discussions for some time to come.

1.1.4 A word about *intelligence*

It is sometimes said by cognitive ethologists (Griffin 1992) and popular writers (e.g., Barber 1994) that animals must be thinking because they behave so intelligently. Indeed, to the nonspecialist one of the most persuasive arguments that animals think as we do is that it is impossible to imagine another explanation for their "clever" behavior (Blumberg and Wasserman 1995; Wynne 2004a). On the whole, however, *intelligence* is not a useful term for describing animal behavior, for two reasons. First, intelligence is generally used to describe global ability in people, whereas the cognitive abilities of animals (and perhaps people as well) are to a large extent modular (Box 2.3). For instance, a Clark's nutcracker that can retrieve thousands of pine seeds months after caching them (Box 1.4) is not necessarily "smart" in other ways. It is particularly good at encoding and retaining certain kinds of spatial information, but it may remember other kinds of information no better than other birds. Within this context, *intelligence* is sometimes used nowadays to refer to the collection of specific cognitive abilities that a species may have (cf., Emery 2006; Pearce 2008).

A second reason to use *intelligence* carefully is that it should be defined formally with respect to a specified goal (McFarland and Bosser 1993). A robot is intelligent with respect to a goal of efficiency if it minimizes use of its battery while when crossing a room. It is intelligent with respect to the goal of remaining intact if it avoids collisions. On this view, biological intelligence should be defined in terms of fitness (Box 1.2 and Kacelnik 2006) or goals such as choosing a good mate that contribute to fitness, and even plants can be intelligent (Trewavas 2002). Sometimes, as we will often see in this book, intelligent behavior may be produced by very "unintelligent" means.

Box 1.2 Natural Selection and Fitness

Evolution, the change in the characteristics of organisms over generations, occasioned much debate before Charles Darwin (1859) and Alfred Russel Wallace explained how it happens. Fossils indicated that very different kinds of animals and plants had existed in the past. Explorers, including Darwin and Wallace themselves, documented how animals and plants in different parts of the world are both similar and different. What Darwin and Wallace did, independently at about the same time, was to show how both the changes in organisms over time and the relationships among them can be explained by a natural cause. That cause is *natural selection,* and it is the inevitable outcome of three fundamental properties of all living things.

1. Offspring inherit their parents' characteristics. Bean seeds produce more bean plants, robin eggs produce more robins, and many of their features will be more like those of their parents than others of the same species. We now know a great deal about the genetic mechanisms involved, but the principle of *inheritance* is independent of such knowledge, which Darwin and Wallace did not have.
2. There is *variation* among individuals within the same species, even when they are closely related.
3. *Selection* takes place. A sea turtle lays hundreds of eggs, an oak tree drops hundreds of acorns, yet the world is not overrun with sea turtles or oak trees. Only those best able to survive in the current environment will live to reproduce. This principle is sometimes summarized as "the survival of the fittest." In technical terms, *fitness* refers to an organism's ability to leave copies of its genes in the next generation, not to what people get at the gym. A male who sires ten healthy offspring is fitter than one who sires two. Because relatives share some of one's own genes, fitness can be enhanced through helping them as well as direct offspring (Chapter 5).

Evolution is the inevitable consequence of inheritance, variation, and selection. Gradually, over many generations, individuals with characteristics that made their ancestors best able to survive and reproduce will come to predominate. Individuals that migrate or are carried into new environments may evolve such different characteristics that eventually their descendents will form a new species, unable to breed with individuals of the ancestral species (see Grant and Grant 2008). Throughout the last part of the twentieth century evolutionary theorists, including most of the founders of behavioral ecology, emphasized selection at the level of the individual, indeed the individual's genes. On this view, the genes best able to program the organisms bearing them to develop into individuals that propagate successfully will be the ones that persist over generations (R. Dawkins 1976, 1995).

However, the logic of inheritance, variation, and selection applies to units at all levels, most importantly for contemporary theorizing, even to groups of individuals. After being emphatically rejected for nearly 40 years, evolution through selection at the level of groups is now becoming accepted as part of a broad theory of multilevel selection (Wilson and Wilson 2007, 2008). Group and individual selection may pull in different ways, but the characters that benefit the group at the apparent expense of the individual may still be advantageous over the long run. Among other things, the force of group selection helps to explain some of the unique features of human psychology such as a tendency to cooperate and empathize with unrelated others (Chapter 12 and Wilson and Wilson 2007, 2008).

Finally, labeling behavior *intelligent* is pretty frankly both anthropomorphic and anthropocentric. Recent demonstrations that species differ in behavioral flexibility, or propensity to adopt novel foraging behaviors (Box 2.2), have revived discussions of overall animal intelligence (cf., Roth & Dicke 2005). This is especially so because the correlation of flexibility with overall brain size and/or size of the forebrain in some animal groups (Box 2.2) satisfies the everyday equation of intelligence with "braininess." The naively anthropocentric nature of such discussions is underlined by a comparison of pigeons and people in a test of complex reaction time (Vickrey and Neuringer 2000). In such a test the subject is confronted with an array of lights; a randomly chosen one, the target, lights up on each trial and the subject's task is to touch it as quickly as possible. Human subjects take longer to respond as the number of lights in the array increases, but people with high IQ show the smallest increase. It is claimed this is because high IQ reflects a general ability to process information fast. On this analysis, " less intelligent" species should be affected more strongly by increasing numbers of targets than humans. In fact, however, pigeons show a smaller effect than very intelligent humans (students at the highly selective U.S. Reed College) tested in the same way, maintaining a fast response speed as target number increases. As the authors of this study observe, "the counterintuitive conclusion follows that pigeons are more intelligent than people. An alternative view assumes that different *intelligences* or factors are employed in different situations by different individuals, groups, and species" (Vickrey & Neuringer, 2000, 291).

1.2 Kinds of explanation for behavior

1.2.1 Tinbergen's four questions

The pioneering ethologist Niko Tinbergen (1963) emphasized that the question, "Why does the animal do that?" can mean four different things, sometimes referred to as "Tinbergen's four whys." "Why?" can mean "How does it work?" in the sense of "What events inside and outside the animal cause it to behave as it does at this moment?" This is the question of the proximate cause (or simply cause) of behavior. Perceptions, representations, decisions, as well as the neural events that accompany them, are all possible proximate causes of behavior (Hogan 2005). One might also ask about development in the individual, that is "How do experience and genetic makeup combine to cause the animal to behave as it does?" "Why" can also mean "What is the behavior good for; what is its survival value?" This is the question of function or adaptive value. Finally, one can ask how a particular behavior evolved, as inferred from the phylogeny of species that show it (Chapter 2) together with evidence about its current function (Cuthill 2005). Causation, development, function, and evolution are not levels of explanation but complementary accounts that can be given of any behavior. As Tinbergen emphasized, a complete understanding of behavior includes answers to all four questions. However, it is important to be clear on how they differ from one another and to avoid confusing the answer to one with the answer to another.

Consider as an example some possible answers to the question raised at the beginning of this chapter, "Why do crows drop walnuts?" The proximate cause of nut dropping would be sought in some interaction of the bird's internal state, most likely hunger, with external stimuli like the presence of walnuts, other crows, and hard surfaces. Proximate causes can be specified at levels right down to events at the level of genes and neurons, but often causal mechanisms are inferred from input-output relations at the level of the whole animal (Hogan 2005). This is generally true with the sorts of cognitive mechanisms discussed in this book. Explanations of the immediate causes of behavior do not include teleology, or reference to conscious purposes or goals (see Hogan 1994a). The future cannot cause what is happening in the present. The crow does not drop walnuts "to get food" though it is possible that she does so because similar behavior in the past was followed by a tasty snack, that is, because of past reinforcement. Examining the bird's history of reinforcement would be part of a developmental explanation, as would an account of any other factors within the crow's lifetime that affected its nut dropping.

The immediate function, or adaptive value, of behavior is what it is good for in the life of the individual. Cracking walnuts clearly functions in obtaining food, but questions about the function of the crow's behavior can also asked at finer levels of detail. For instance, the functional question, "Why carry a nut so high and no higher?" was tackled by testing whether the height to which nuts are carried matched the type of nut and where it was dropped (Figure 1.1, see also Zach 1979).

Tinbergen's fourth question, "How did it evolve?" usually has to be tackled by trying to look at the behavior's phylogenetic history using methods described in Chapter 2. For the crows' nutcracking, this would include discovering whether close relatives of American crows also drop hard-shelled prey items and whether specific ecological conditions are associated with prey-dropping (Cristol and Switzer 1999). Occasionally it has been possible to observe evolution happening in the wild as natural populations have changed rapidly in response to changes in selection pressures (e.g., Endler 1986). Some of these examples involve behavior at least implicitly. For instance, in a famous long-term field study, Rosemary Grant and Peter Grant observed the beaks of seed-eating finches on the Galapagos Islands changing in response to drastic changes in rainfall (Grant and Grant 2008). In years of drought, only the birds most skilled at cracking the few remaining seeds could survive and reproduce. Beak depth, an indication of seed-cracking power, contributed importantly to survival in the medium ground finch (*Geospiza fortis*). Because beak depth is heritable, changes in the population's distribution of beak depths could be detected in a few generations (Figure 1.2). The birds' behavior must have changed, too, perhaps through learning. Rather than ignoring the hardest seeds, as they did in times of plenty, the successful individuals evidently became skilled at finding and cracking them.

In terms of Tinbergen's four questions, cognition is one of the proximate causes of behavior. Because studying cognition may include analyzing how information and ways of responding to it are acquired, studying cognition may also involve studying development. Throughout this book we will be concerned with the adaptive value

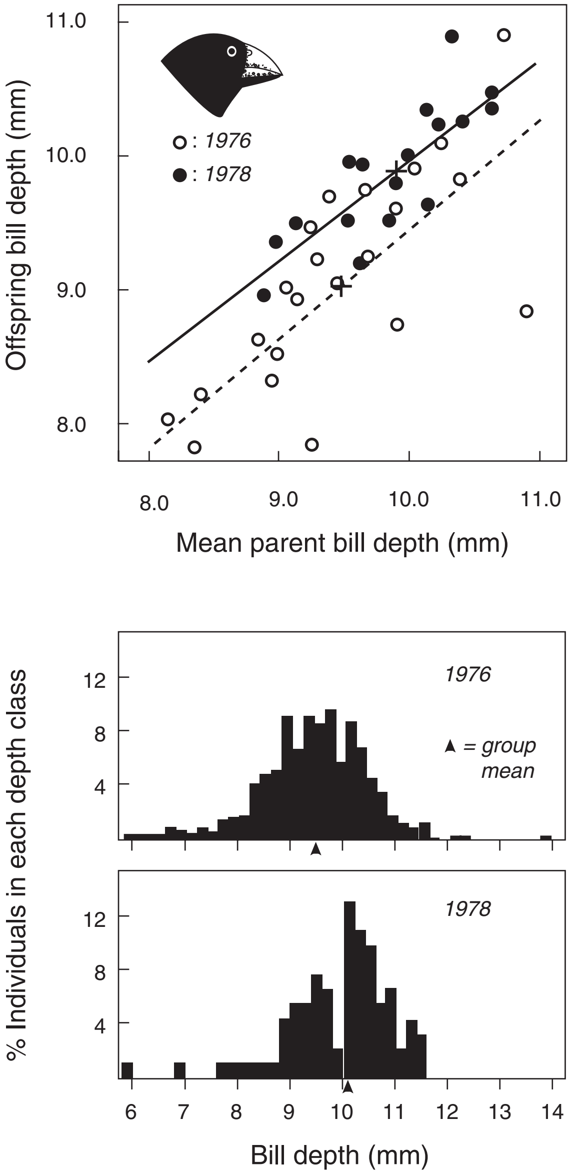

Figure 1.2. Upper panel: Inheritance of bill depth (height of the bill in the drawing) in medium ground finches in two different years. Slope of the line relating offspring to parent bill depth—a measure of heritability—was almost the same in both years. Variation and selection of bill depth are illustrated in the two lower panels. In 1978 there was a drought, and the finches could subsist only by cracking the hardest seeds, accounting for the greater survival of those with deeper bills. Redrawn from Boag and Grant (1984) and Boag (1983) with permission.

and evolution of cognitive mechanisms. But speaking of cognition doesn't imply that animals are aware of the effects that their actions have on fitness. Evolution produces machines that reproduce themselves (Box 1.2). A robin builds a nest and lays eggs. It responds to eggs by incubating them. As a result of the parents' keeping the eggs at a temperature they have evolved to develop at, young robins hatch with nervous systems so constructed that they open their beaks and beg when an adult approaches the nest. The adult's nervous system responds to gaping by inserting food, and so on. The bird isn't responding to "my young," let alone planning to have lots of grandchildren, but to stimuli that are generally reliable correlates of offspring like gaping mouths in its nest. Behavioral mechanisms, including cognitive processes such as memory for the location of the nest and tuning of the adults' perception to the signals emitted by the young, are selected if they increase their bearer's representation in future generations, but such mechanisms need not—and seldom, if ever, do—include foresight into the effects of behavior on fitness (Chapter 11).

1.2.2 "Learned" and "innate" behavior

Learning is often contrasted with genetic or innate control of behavior. What this dichotomy overlooks is that learning is possible only for an animal whose genes and prior environment have resulted in development of an individual ready to be affected by experience in a certain way. No behavior is either strictly learned or entirely innate. An excellent illustration of how preexisting selective processes in the animal interact with specific experiences to produce learning comes from classic comparisons of song learning in two species of sparrows (Marler and Peters 1989). Like many other songbirds (Box 13.2), male song sparrows (*Melospiza melodia*) and swamp sparrows (*Melospiza georgiana*) need to hear species-specific song early in life in order to sing it when they mature. The two species are closely related, but swamp sparrows sing a much simpler song.

Marler and Peters played song sparrow songs and swamp sparrow songs to isolated young males of both species in the laboratory. Thus, all the birds had the same acoustic experience. But their behavior as adults revealed that they had learned different, species-appropriate things from it (Figure 1.3). Swamp sparrows learned only swamp sparrow songs, and song sparrows had a strong preference to learn song sparrow songs. The interaction of species with experience is still seen even when the birds are raised in the laboratory from the egg or very early nestling stage, showing that it probably does not result from birds hearing their father's song. Because birds of each species sometimes do produce sounds characteristic of the other species, it seems unlikely that the species difference in song production results from a motor constraint. In the wild, these two species may live within earshot of each other, so early-developing selectivity in perception and/or learning likely functions to ensure that each one learns only its own species song. Indeed, young birds still in the nest respond most to their own species song, as shown by the way heart rate changes when they are played different sounds (Marler and Peters 1989).

This example comes from a specialized behavior shown by only a few of the world's species, but it makes a very important general point: cognitive mechanisms are adaptations to process and use certain kinds of information in certain ways, not mechanisms for information processing in general. As for the theme of this section, insofar as it implies that genes can work without an environment to work in, the term *innate* is never appropriate in modern biology (Bateson and Mameli 2007). However, we do sometimes need a term for the many behaviors that appear in development ready to serve their apparent function before they can have done so. For instance, selecting the species-typical song for learning clearly serves the function of allowing the adult male, many months later, to sing in a way that his conspecifics are most responsive to. Hogan (1994b) has suggested the term *prefunctional* for such cases, because it does not imply that the genes have worked in isolation nor that prior experience is irrelevant. However, because this term implies that we know the function of the behavior, *predisposition* or *preexisting bias* may be preferable.

Finally, to say that some behavior or cognitive process develops prefunctionally is not to say that it is unmodifiable (Dawkins 1995). As the comparison of song and swamp sparrows illustrates, how much and in what ways behavior can be modified

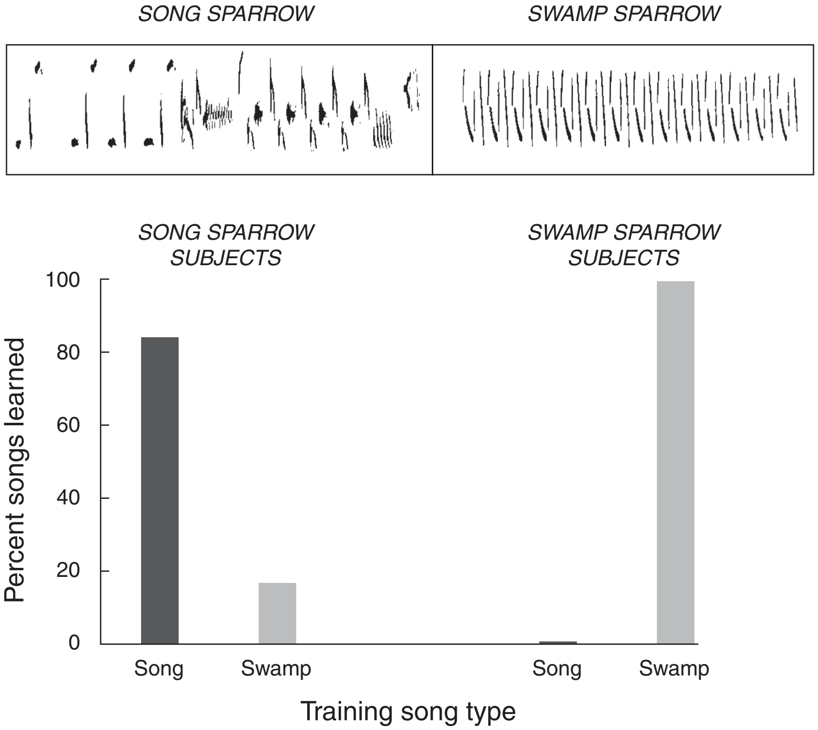

Figure 1.3. Song sparrows and swamp sparrows exposed to both song sparrow and swamp sparrow songs when young learn primarily the songs of their own species. Top panel shows sonagrams (sound frequency vs. time) of songs from normal adults of the two species. Redrawn from Marler and Peters (1989) with permission.

itself reflects events earlier in development. This example also shows how a stereotyped behavior seen in most normally developing members of a species can result from learning. However, although it makes a key point for this book in showing how experience can have species-species effects, it misleadingly implies that effects of experience (here, the songs) and genes (the species of sparrow) can always be neatly separated. Developmental biologists are increasingly documenting gene by environment interactions and interdependencies as well as epigenetic effects, in which environmental effects on the genes of one generation are passed on to the next (Sokolowski & Levine in press). Some of these discoveries have implications for behavior; undoubtedly more such will be uncovered in the future.

In conclusion, structure as well as behavior, the animal's *phenotype,* results from a continuous and seamless interplay of genes and environment that is itself selected. The extent to which behavior patterns or cognitive capacities are modifiable by experience varies so much as to make the terms *learned* and *innate* (or *nature* and *nurture*) obsolete (Bateson and Mameli 2007). The fact that individuals within a species (i.e., with a common *genotype*) may develop different physical and/or behavioral phenotypes in different environments is known as *phenotypic plasticity.* The ability of individuals to learn details of their own environment that are unpredictable on an evolutionary timescale is but one aspect of the more general phenomenon of adaptive phenotypic plasticity (Dukas 1998; for a brief review see Agrawal 2001; for further discussion of the topics in this section see Marler 2004).

1.3 Approaches to comparative cognition

Psychologists and biologists have traditionally taken different approaches to studying learning and cognition in animals. These two contrasting traditions have been called, among other things, the study of general processes and the study of adaptive specializations (Riley and Langley 1993) or the General Social Science Model and evolutionary psychology (Cosmides and Tooby 1992). Psychologists have tended to ask, "Can animals do what people do, and if so how do they do it?" whereas biologists tend to ask, "Why, in all Tinbergen's four senses, do animals do what they do in the wild?" Thus the contrast between traditional psychological and biological approaches is one between anthropocentric, or human-centered, and ecological, animal-centered, approaches. It is also one between a field centered on mechanism, just one of Tinbergen's four questions, and one in which "Nothing makes sense except in the light of evolution" (see e.g., Plotkin 2004)

1.3.1 The anthropocentric approach

Comparative psychology began with Darwin's claim—profoundly shocking at the time—that humans are similar to other species in mental as well as physical characteristics. Chapter 3 of his second book, *The Descent of Man and Selection in Relation to Sex* (Darwin 1871), touches on almost every problem that has been studied by comparative psychologists since. In it, Darwin claimed that other animals differ cognitively from humans in degree but not in kind. That is to say, animals share human abilities such as reasoning, memory, language, and aesthetic sensibility, but generally they possess them to a lesser degree (see Chapter 15). His emphasis was on continuity among species rather than diversity, the other side of the evolutionary coin (Rozin and Schull 1988). Acceptance of continuity has led to using animals in psychology as little furry or feathery people, model systems for studying general processes of learning, memory, decision-making, even psychopathology and their neural and genetic underpinnings. Thus this approach can be characterized as *anthropocentric* because it is concerned primarily with issues related to human psychology.

Around the beginning of the 1900s psychologists' study of cognitive processes in animals began to focus on associative learning (see Boakes 1984). Some researchers in the first part of the twentieth century did study issues such as animal reasoning or insight learning (Dewsbury 2000), but animal cognition as a recognized subfield did not take off until the 1970s (Hulse 2006). Its practitioners were concerned to distinguish themselves from S-R psychologists, who explained behavior in terms of connections between stimuli and responses established by classical or instrumental conditioning and eschewed speculation about unobservable processing of information. Psychologists studying animal cognition, in contrast, used behavior as a window onto processes of memory and representation (Wasserman 1984). Initially, much of their research used learned behavior of rats and pigeons in the laboratory to analyze processes that were being successfully studied in people, such as memory for lists of items, concept formation, and attention (cf., Hulse, Fowler, and Honig 1978).

Research on animal cognition based on the anthropocentric approach has three important characteristics. First, it focuses on memory, representation, and other kinds of information processing that can be identified in people. Second, such research is implicitly comparative, in that other species like parrots or pigeons are compared with humans, but the choice of species is often based more on convenience than on evolutionary considerations. Finally, traditional discussions of anthropocentric research were pervaded by the incorrect and misleading notion of a phylogenetic scale or *scala naturae* (Hodos and Campbell 1969). This is the idea that evolution is a continuous ladder of improvement, from “lowly” worms and slugs, through fish, amphibians and reptiles, to birds and mammals. Humans, needless to say, are at the pinnacle of evolution in this scheme. But present-day species cannot be lined up in this way (Chapter 2). People are not more highly evolved fish, birds, rats, or even chimpanzees. Correct inferences about the relationship between cognitive or brain processes in humans and those in nonhumans depend on a detailed appreciation of the biology of “animal models” (Preuss 1995 ; Papini 2008). Nevertheless, studying a few very diverse species, as in the research sketched in Box 1.3, may be the best way to reveal processes general to all species (Bitterman 2000; Papini 2002). Exactly this approach to genome mapping has provided stunning support for generality: species as

Box 1.3 Traditional Comparative Psychology: An Example

In the 1960s and 1970s, M. E. Bitterman and his associates carried out an extensive program of research comparing the performance of goldfish, painted turtles, pigeons, rats, and monkeys on a number of standard laboratory tasks (Bitterman 1965, 1975). Later, this work was extended to honeybees (see Bitterman 2000). Their overall aim was to test the assumption that the “intelligence” of “lower” animals differed only in degree and not in kind from that of “higher” animals. Of course, as Bitterman (1975, 2000) recognized, these species are not on an evolutionary ladder but at the ends of separate branches of the tree of life (Figure B1.3). Therefore, commonalities must reflect either their presence in some very ancient common ancestor or convergence due to similar environmental pressures

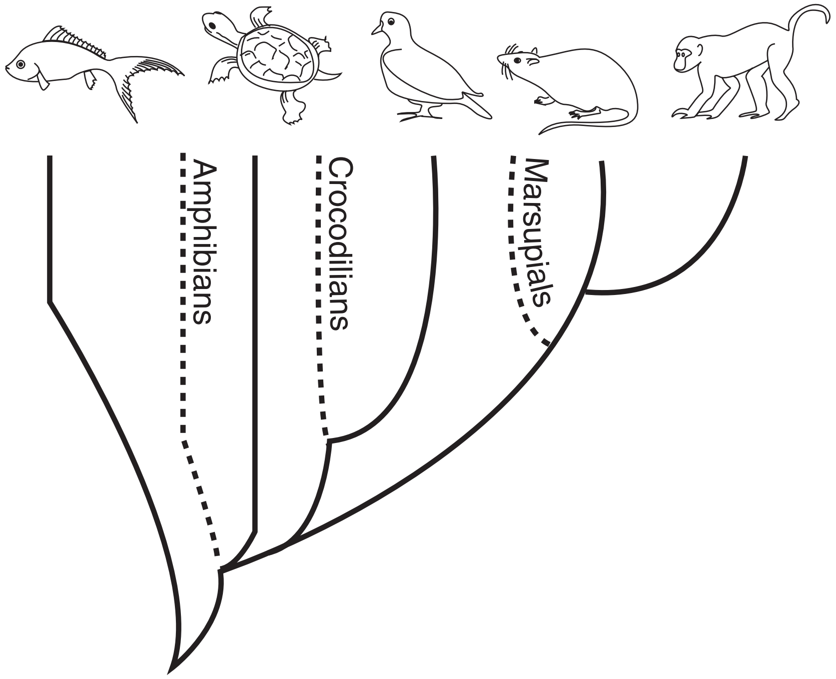

Figure B1.3. A simple phylogeny (see Chapter 2) of the species tested by Bitterman and his colleagues in comparative studies of learning. Neither the recency with which one group is thought to have diverged from another nor its left-right arrangement in such a diagram necessarily implies anything about “intelligence.” Redrawn from Bitterman (1975) with permission.

Bitterman devised ingenious versions of standard apparatuses to present the same kinds of tasks to these very different species. Fish pushed paddles for a reward of worms; pigeons pecked lighted disks for a few grains of corn; turtles crawled down small runways. In one series of experiments, the animals were compared on their ability to learn *successive reversals* of simple visual and spatial discriminations. In successive reversal (Chapter 6) an animal is first rewarded for choosing a certain one of two simultaneously presented stimuli, say red rather than green. After a number of trials, the rewarded stimulus is reversed, for example, the animal must choose green rather than red, and so on. "Intelligent" behavior is to improve over successive reversals, eventually performing perfectly after just one trial on each new problem. Within each species, performance on visual discriminations (e.g., red vs. green for species with color vision or black vs. white for those without) was also compared to performance on spatial (e.g., left vs. right) discriminations. Monkeys, rats, and pigeons improved on both visual and spatial reversals, fish improved on neither, and turtles improved on spatial but not visual reversals. What results from this kind of selection of species and problems can reveal about "the evolution of intelligence" is discussed further in Chapter 2 (see also Papini 2002, 2008).

diverse as fruitflies, mice and humans are turning out to share unexpected numbers of genes and basic developmental processes (see Robinson 2004; Papini 2008). In addition, the rigorous methodology and the principles developed with traditional psychological studies of animals are essential to more biologically focused research (e.g., Timberlake, Schaal, and Steinmetz 2005).

1.3.2 Anthropocentrism, anthropomorphism, and Morgan's Canon

Documenting human-like "mental powers" of animals was central to the agenda of early defenders of Darwinism. Similarity between human and animal minds would surely be the most convincing evidence of evolutionary continuity between humans and other species. Accordingly, some of Darwin's supporters, primary among them George Romanes (1892) set out to collect anecdotes appearing to prove animals could think and solve problems the way people do. Their approach was not just anthropocentric but frankly *anthropomorphic,* explaining animals' apparently clever problem solving in terms of human-like thinking and reasoning. But as we have seen in the case of the nutcracking crows, just because an animal's behavior looks to the casual observer like what a person would do in a similar-appearing situation does not mean it can be explained in the same way. Such reasoning based on analogy between humans and other animals must be tested with experiments that take into account alternative hypotheses (Heyes 2008).

Fortunately for progress in understanding animal cognition, critics of extreme anthropomorphism were not slow to appear. E. L. Thorndike's (1911/1970) pioneering experiments on how animals solve simple physical problems showed that gradual learning by trial and error was more common than human-like insight and planning (Galef 1998). C. Lloyd Morgan also observed animals in a systematic way but is now best known for stating a principle commonly taken as forbidding unsupported anthropomorphism. What Morgan (1894) called his Canon states, "In no case may we interpret an action as the outcome of the exercise of a higher psychical faculty, if it can be interpreted as the outcome of the exercise of one which stands lower in the psychological scale." Morgan's Canon is clearly not without problems (Sober 2005). What is the "psychological scale"? Don't "higher" and "lower" assume the phylogenetic scale? In contemporary practice "lower" usually means associative learning, that is, classical and instrumental conditioning or untrained species-specific responses. "Higher" is reasoning, planning, insight, in short any cognitive process other than associative learning.

For an example of how Morgan's Canon might be applied today, suppose, contrary to the data in Figure 1.1, that crows had been found to drop nuts in front of cars more than on the empty road. An obvious "simple" explanation is that they had been reinforced more often when dropping a nut when a car was coming than when the road was empty and thereby had learned to discriminate these two situations. A "higher," anthropomorphic, explanation might be that having seen fallen nuts crushed by cars the insightful crows reasoned that they could drop the nuts themselves. The contrast between these explanations suggests a straightforward test: observe naïve crows to see if the discrimination between approaching cars and empty roads develops gradually (supporting the "simple" explanation) or appears suddenly, without any previous trial and error (supporting the "higher" explanation). Unfortunately, competing explanations do not always make such readily discriminable predictions about observable behavior. Even when they do, experiments designed to pit them against each other may not yield clear results. Then agnosticism may be the most defensible policy (Sober 2005).

In practice, the field of comparative cognition as it has developed in the past 30–40 years has a very strong bias in favor of "simple" mechanisms (Sober 2001; Wasserman and Zentall 2006a). The burden of proof is generally on anyone wishing to explain behavior in terms of processes other than associative learning and/or species-typical perceptual and response biases. To many, anthropomorphism is a dirty word in scientific study of animal cognition (Mitchell 2005; Wynne 2007a, 2007b). But dismissing anthropomorphism altogether is not necessarily the best way forward. "Anthropodenial" (de Waal 1999) may also be a sin. After all, if other species share common ancestors with us, then we share an a priori unspecifiable number of biological processes with any species one cares to name. Thus in some ways, as Morgan apparently thought (Sober 2005), the simplest account of any behavior is arguably the anthropomorphic one, that behavior analogous to ours is the product of a similar cognitive process. Note, however, that "simple" has shifted here from the cognitive process to the explanation (Karin-D'Arcy 2005), from "simpler for them" to "simpler for us" (Heyes 1998).

Where do these considerations leave Morgan's Canon? A reasonable modern interpretation of the Canon (Sober 2005) is that a bias in favor of simple associative explanations is justified because basic conditioning mechanisms are widespread in the animal kingdom, having been found in every animal, from worms and fruitflies to primates, in which they have been sought (Papini 2008). Thus they may be evolutionarily very old, present in species ancestral to all present-day animals and reflecting adaptations to universal causal regularities in the world and/or fundamental properties of neural circuits. As species diverged, other mechanisms may have become available on some branches of the evolutionary tree, and it might be said to be the job of comparative psychologists to understand their distribution (Papini 2002).

But for such a project to make sense, it must be clear what is meant by associative explanations and what their limits are. Associative learning, discussed in depth in Chapter 4, is basically the learning that results from experiencing contingencies, or predictive relationships, between events. At the theoretical level, such experience in Pavlovian (stimulus-stimulus) or instrumental (response-stimulus) conditioning has traditionally been thought of as strengthening excitatory or inhibitory connections between event representations. Thus one might say that any cognitive performance that does not result from experience of contingencies between events and/or cannot be explained in terms of excitatory and/or inhibitory connections is nonassociative. Path integration (Chapter 8) is one example: an animal moving in a winding path from home implicitly integrates distance and direction information into a vector leading straight home. As another, on one view of conditioning (Section 4.5.2) the flow of events in time is encoded as such and computed on to compare rates of food presentation during a signal and in its absence. Other nonassociative cognitive processes which might be (but rarely if ever have been) demonstrated in nonhumans include imitation, that is, storing a representation of an actor's behavior and later reproducing the behavior; insight; and any kind of reasoning or higher-order representations or computations on event representations. As we will see throughout the book, discriminating nonassociative "higher" processes from associative ones is seldom straightforward, in part because the learning resulting from associative procedures may have subtle and interesting cognitive content. In any case, the goal of comparative research should be understanding the cognitive mechanisms underlying animal behavior in their full variety and complexity rather than partitioning them into rational or nonassociative vs. associative (Papineau and Heyes 2006).

In conclusion, neither blanket anthropomorphism nor complete anthropodenial is the answer (Mitchell 2005). Evolutionary continuity justifies anthropomorphism as a source of hypotheses. When it comes to comparing human cognition with that of other species, it is most likely that—just as with our genes and other physical characters—we will find some processes shared with many other species, some with only a few, and some that are uniquely human. One of the most exciting aspects of contemporary research on comparative cognition is the increasing detail and subtlety in our picture of how other species' minds are both like and not like ours.

1.3.3 Biological approaches to animal behavior

While experimental animal psychology was flourishing in North America, ethology was developing in departments of zoology in Europe (Burkhardt 2005). Guided by Tinbergen's four questions and the vision of developing a biological science of behavior distinct from psychology, ethologists emphasized the behavior of animals in the wild. They studied a wide range of species: insects, birds, and fish as well as mammals. Behavior was seen to be as much a characteristic of a given species as its coloration or the structure of its body (Lorenz 1941/1971; Tinbergen 1959). In an effort to break free of sentimental attitudes toward animals, ethologists emphasized the same objective behaviorist approach as Skinner and other experimental psychologists. For instance, at the very beginning of his textbook *The Study of Instinct* Tinbergen (1951, 4) warns, "Because subjective phenomena cannot be observed directly in animals it is idle either to claim or to deny their existence. Moreover to ascribe a causal function to something that is not observable often leads to false conclusions."

In the 1960s and 1970s the ethological study of the adaptive value and evolution of behavior developed into the field of behavioral ecology (Krebs and Davies 1993; Cuthill 2005). Behavioral ecology, or sociobiology (Wilson 1975), is characterized by an attempt to predict behavior from first principles of evolutionary biology using explicit models of the consequences of behavior for fitness. Like ethologists, behavioral ecologists focus on behavior of animals in the field and study a wide variety of species, but initially they were concerned almost exclusively with the functional and evolutionary "why" questions. Early research in behavioral ecology aimed to discover simply whether or not behavior had the properties predicted by evolutionary models. For example, did redshank or some other bird choose food items optimally? As the field developed, and at about the same time as some psychologists (e.g., Kamil 1988; Shettleworth 1993) were advocating analyses of ecologically meaningful aspects of cognition, behavioral ecologists began to appreciate the role of cognitive mechanisms in producing or failing to produce the predicted behaviors (e.g., Stamps 1991; Huntingford 1993; Dukas 1998; Chittka and Thomson 2001). They began to ask, for example, about the processes of perception, learning, and choice that lead the redshank to select its prey and how these play a role in the bird's making, or failing to make, optimal choices (Chapter 11). The integration of cognitive psychology with the study of how animals solve ecologically important problems was referred to as *cognitive ecology* (Real 1993; Dukas 1998; Healy and Braithwaite 2000). *Sensory ecology* (Dusenbery 1992) and *neuroecology* (Bolhuis and Macphail 2001; Sherry 2006), were coined for the study of how sensory systems and brain architecture, respectively, are matched to species-specific environmental requirements.

1.3.4 Convergence and synthesis: Comparative cognition in the twenty-first century

Ethologists, behavioral ecologists, and traditional comparative psychologists emphasize different questions about animal behavior and tend to do their research in different settings and on different species, but their fields are clearly related. It stands to reason that data and theory of each of these fields should illuminate issues being studied by the others. Within psychology, this point of view led to what has been called the ecological or synthetic approach to comparative cognition (Kamil 1988; Shettleworth 1993). Unlike the anthropocentric or general process approach, the ecological approach emphasizes studying how animals use cognition in the wild, for example in foraging or finding their way around. Species are chosen on the basis of behavior indicating some particularly interesting cognitive processing such as the ability to home over long distances, use tools, keep track of relationships in a large social group, or remember the locations of large numbers of food items (Box 1.4). The ecological approach includes explicitly comparative studies designed to analyze the evolution and adaptive value of particular cognitive abilities. The species compared may be close relatives that face different cognitive demands in the wild and therefore are expected to have diverged in cognitive ability. Alternatively, species may be compared that are not very close relatives but face similar cognitive demands in the wild. Such species are expected to have converged in the ability of interest. Data about natural history and evolution are an integral part of this kind of comparative psychology, but so are theories and methods developed with the anthropocentric approach. This approach is increasingly shared by biologists trying to understand cognitive processes underlying behaviors they observe in wild animals (e.g., Bluff et al. 2007; Cheney and Seyfarth 2007).

Cognitive ecology, sensory ecology, cognitive ethology, neuroecology, evolutionary psychology, ecological comparative psychology: whatever these enterprises are called, they all have in common the assumption that cognition is best understood by being studied in the context of evolution and ecology, that is, as a biological science. Together they have been converging into a vigorous interdisciplinary field of comparative cognition research. Kamil (1998) suggested that *cognitive ethology* should be reclaimed from those who use it to refer to studies of conscious processes in animals to refer to this synthetic research program. Reasonable though this

Box 1.4 Food Storing Birds and the Ecological Approach

Some species of birds store food in the wild and use memory to find it again. One of the most remarkable is the Clark's nutcracker (*Nucifraga columbiana*) of the American Southwest (Figure B1.4). Nutcrackers bury thousands of caches of pinon pine seeds in the late summer and dig them up from beneath the snow throughout the winter and into the next spring (Balda and Kamil 2006). Early observers of food-storing in corvids (jays, crows, and nutcrackers) and parids (chickadees and titmice) found it incredible that these birds might be able to remember the locations of caches. Perhaps they were just raising the general level of availability of food for all birds in the area. But food-storing would be unlikely to evolve unless the individuals doing it have greater fitness than lazy individuals which simply eat the food stored by others (Andersson and Krebs 1978). As this argument suggests, food storing birds do retrieve their own caches, and they use memory to do it (Shettleworth 1995).

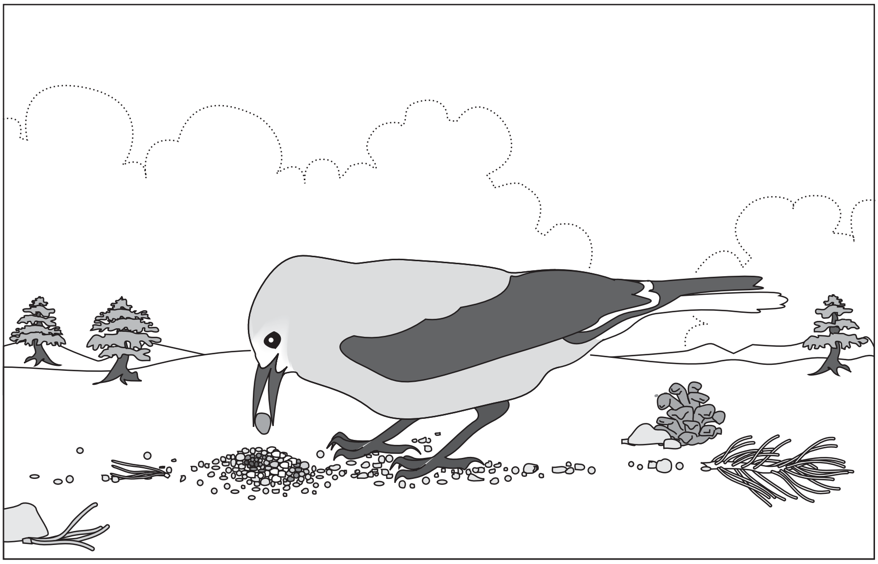

Figure B1.4. A Clark's nutcracker burying a seed. A bird generally caches several seeds in each site. From a photograph by R. P. Balda.

The fact that food-storers must remember the locations of a large number of items for days, weeks, or months suggests that along with the specialized behavior of caching food they may have evolved an enhancement of some aspect of memory. For example, maybe they can remember more items of spatial information for longer than other birds. Within both the corvids and the parids, some species store more food than others, so this hypothesis can be tested by comparing memory within each bird family. Corvids or parids that store more do tend to have better spatial memory, and the hippocampus, a part of the brain involved in spatial memory, is bigger relative to brain and body size in food storers than in nonstoring species. Both the data and the thinking behind these conclusions have proven controversial, as discussed in Chapter 2. Nevertheless, research on food-storing birds is still a good example of how information from evolutionary biology, field studies, neurobiology, psychological theories about memory, and techniques for testing memory in the laboratory can all be integrated to provide new insights.

suggestion may be, it does not seem to have been widely adopted (Allen 2004), and the term *comparative cognition* is generally used here. The present trend toward interdisciplinary research is a major departure from a century or more in which psychological research with animals (including often the human animal) has been largely divorced from, or even hostile to, the rest of the biological sciences and the framework provided by evolution (Richards 1987; Plotkin 2004). For more than 50 years, comparative psychologists (e.g., Beach 1950; Hodos and Campbell 1969) have been complaining about the detrimental effects of this divorce on psychological research with animals. Is the field itself evolving at last? There is plenty of evidence that it is. To some extent this evolution reflects the fact that psychology in general is becoming better integrated with the rest of the biological sciences, impelled by the apparent success of neuroscience and genetics in illuminating mechanistic underpinnings of behavior (e.g., Lickliter and Honeycutt 2003). But it also reflects the excitement generated by a variety of specific research programs that approach questions about animal cognition in a comprehensive biological framework.

For example, the last 20 years or so have seen the development of a lively cross-disciplinary field of research and theorizing on comparative social learning and possible precursors of human culture (Zentall and Galef 1988; Heyes and Galef 1996; Reader and Laland 2003; Galef and Heyes 2004; Richerson and Boyd 2005). Anthropocentrism has been turned on its head as studies of animal tool using, theory of mind, cultural transmission of skills, episodic memory and other capacities traditionally thought to be unique to humans are seen as relevant to understanding human cognitive evolution and development (e.g., Gomez 2005; Penn et al. 2008). The study of spatial behavior is increasingly interdisciplinary, embracing field and laboratory research on brain, behavior, and ecology of species as diverse as honeybees, ants, rats, and people (Gallistel 1990; Healy 1998; Jeffery 2003). Behavioral ecologists are embracing mechanistic studies at the level of the brain (Giraldeau 2004). Textbooks of animal behavior (e.g., Dugatkin 2004; Bolhuis and Giraldeau 2005) include sections on learning and animal cognition. The International Comparative Cognition Society, which began in 1994 as a small group of experimental psychologists mainly working with rats and pigeons, now represents researchers from psychology, biology, and anthropology studying most of the species and issues discussed in this book. As we see throughout the book, such convergence of researchers from different traditions, accustomed to focusing on different ones of Tinbergen's questions, can lead to misunderstanding and controversy, as when cognitive psychologists and behavioral ecologists disagree about what counts as *teaching* (Chapter 13), but it has also immeasurably broadened and enriched the field.

1.3.5 Comparative cognition and other areas of the behavioral and brain sciences

The comparative study of cognition intersects with many other areas of the behavioral and brain sciences. These include neuroscience, genetics, evolutionary psychology, developmental psychology, anthropology, conservation, and animal welfare. The research perhaps most closely connected to that discussed in this book concerns the neurobiological and molecular mechanisms of learning and cognition. By far the majority of studies of learning in animals at the present time are being done in this context (Domjan and Krause 2002). As Skinner wrote in *The Behavior of Organisms,* "a rigorous description at the level of behavior is necessary for the demonstration of a neurological correlate" (Skinner 1938, 422; Timberlake, Schaal, and Steinmetz 2005). So, for example, when researchers engineer a mouse strain that develops neurological symptoms of Alzheimer's disease (Chen 2000), deciding whether those mice show memory impairments analogous to those seen in human Alzheimer's sufferers depends crucially on having appropriate behavioral tests of memory, as well as knowledge of mouse behavior (Gerlai and Clayton 1999). Here, however, we will be concerned with research on neuroscience and genetics only when it impinges on the understanding of cognitive processes as such.

Evolutionary psychology is also closely related to some topics in the present book. Evolutionary psychology is based on the premise that principles of cognition and behavior in humans are adaptations to social and environmental demands throughout evolution (Barkow, Cosmides, and Tooby 1992; Barrett, Dunbar, and Lycett 2002; Dunbar and Barrett 2007). For example, reasoning ability may have evolved at least in part to deal with social obligations in early hominid groups (Cosmides 1989). Evolutionary psychology has generated some controversial findings (see Buller 2005). One of its weak points is that its hypotheses often have to be based on conjectures about the conditions present early in human evolution. In this respect, research on the evolution of cognition in other animals is on much firmer ground because other species' present-day environments are likely much more representative of their past environments than is the case for humans. Hypotheses about evolution and adaptation can also be tested more directly in other species than in humans by comparing groups of present-day species. Thus research with nonhuman species can provide well-grounded hypotheses for testing in humans as well as a model for how such hypotheses should be tested (Daly and Wilson 1999). Indeed, the subject of this book might be described as evolutionary psychology "in the round" (i.e., in the broad sense, see Heyes 2000).

Some contemporary researchers directly address questions about the evolution of human cognition through studies with other species, for example seeking to combine insights from genetics, neurobiology, anthropology, child development, field studies of primate behavior, and laboratory tests to understand the fundamental question of what makes us different from even our closest living relatives, the chimpanzees and other primates (Chapter 15 and Gunter et al. 2005). This is particularly true in the study of spatial, numerical, and social cognition (Chapters 8, 10, and 12). Communication between comparative and developmental researchers is partly explained by the fact that those who study very young children share a problem faced by those studying animals—their subjects can't talk—making methods easily transferred between fields. It is also commonly assumed that any cognitive abilities chimpanzees share with us are most likely to be those shown by very young children (cf., Matsuzawa 2007).

Finally, the results of research on comparative cognition can have implications for conservation and animal welfare. For example, when members of an endangered species are raised in captivity to be released in the wild, it may be important to understand what they would have learned normally and figure out how to impart such knowledge to captive-reared individuals. This can include what predators to avoid (Griffin, Blumstein, and Evans 2000; Griffin 2004) and what cues indicate a suitable habitat (Stamps and Swaisgood 2007). When it comes to animal welfare, there is a widespread sentiment that the more research shows that animals are like us, the more we should value and protect them (but see Wynne 2004b). Whatever one's point of view in this controversial area, knowledge about animal behavior and cognition can be applied to better understand and thus improve the welfare of both wild and captive animals (see Fraser and Weary 2005; Dawkins 2006).

1.4 Summary

Studying cognition means analyzing how animals acquire, process, and use information. Most people who study comparative cognition remain agnostic as to whether animals process information consciously or not. Some animals may be conscious in some sense, but we cannot know because consciousness refers to a private subjective state. Furthermore, it is often difficult to specify any behavior uniquely resulting from consciousness. How animals process information and behave adaptively can be understood, and on the whole should be studied, without reference to consciousness. Nevertheless, some researchers are of the opinion that some animals are undoubtedly conscious, and scientists should be trying to understand the nature of their conscious states.

Four questions, often referred to as Tinbergen's four whys, can be asked about any behavior. These are questions about immediate causation, development in the individual, present-day function, and evolution. The four questions are complementary; each contributes to a complete understanding of behavior. Cognitive mechanisms such as perception and memory are among the immediate causes of behavior; learning is part of behavioral development. Cognitive processes are also part of an animal's adaptation to its environment and therefore must have evolved through natural selection.

Cognition in nonhuman species has traditionally been approached differently by psychologists than by biologists. Psychologists have tended to take an anthropocentric approach, seeking to understand humanlike performance in other species and perhaps interpreting their findings by reference to an assumed phylogenetic scale. Anthropocentrism is not the same as anthropomorphism, or interpreting animal behavior as if it was caused by humanlike thought processes. Explicit anthropomorphism is thought to have been rejected with the adoption of Morgan's Canon early in the 1900s, but cannot be done away with entirely. The ecological or biological approach to cognition consists of analyzing the kinds of information processing animals do in situations of ecological importance like foraging, choosing mates, finding their way around. With this approach, species are compared with reference to evolutionary and ecological relationships. After a long history in which comparative psychology developed largely independently of biological studies of behavior, contemporary research on comparative cognition is increasingly integrating these two approaches and making rich connections with other biological sciences.

Further reading and websites

The whole field of comparative cognition is covered in recent books including introductory texts by Wynne (2001) and Pearce (2008), the books edited by Balda, Pepperberg, and Kamil(1998); Heyes and Huber (2000); Wasserman and Zentall (2006b); and Bekoff, Allen, and Burghardt (2002), and the March, 2009, special issue of *Behavioural Processes* (vol. 80, no. 3). Hauser's (2000) *Wild Minds* and Wynne's (2004a) *Do Animals Think?* are excellent popular books by researchers in the field. Donald Griffin regularly updated his proposals about animal consciousness (Griffin 1976) almost until the end of his life (Griffin 2001). The animal behavior texts by Bolhuis and Giraldeau (2005) and Lucas and Simmons (2006) both cover topics included in this book, as does *Congnitive Ecology II* (Dukas and Ratcliffe, 2009). Papini's (2008) *Comparative Psychology* provides comprehensive background on the evolution of brain and behavior. *Behavioural Ecology* (Danchin, Giraldeau, and Cezilly 2008) is a comprehensive overview of that field.

From Darwin to Behaviorism (Boakes 1984) and the books by Richards (1987), Plotkin (2004), and especially Burkhardt (2005) are recommended for the history of thought and research in comparative psychology and ethology. *Tinbergen's Legacy*

(Verhulst and Bolhuis 2009) reprints Tinbergen's 1963 paper along with the contemporary discussions of the four questions that were originally published in 2005 in *Animal Biology*. For animal consciousness, the writings of Dennett (1996), Allen and Bekoff (1997), Carruthers (e.g., 2005), and Sober (e.g., 2005) are useful; the chapter by Heyes (2008) is exceptionally clear on this and other issues. Kennedy's (1992) little book is a stimulating analysis of what he saw as the insidious influence of anthropomorphism. The discussions accompanying Wynne's (2007a) paper make clear that it is still controversial.

Most of the active scientists whose research is discussed in this book have lab websites with further information about their work. Many such websites and online editions of journals have links to video illustrations. These can be both entertaining and wonderful aids to understanding. The Animal Behavior Society and the Comparative Cognition Society both have comprehensive websites with links to researchers' sites, news, and events in the area. Given the ease with which these resources can be located, on the whole this book does not include specific references to online material.

2

Evolution, Behavior, and Cognition: A Primer

Thanks to the admonitions of writers like Hodos and Campbell (1969) and Beach (1950), comparative psychologists have largely stopped interpreting species differences in terms of the *scala naturae*. Arguably, however, more sophisticated evolutionary thinking has yet to take its place (Papini 2002). This chapter introduces contemporary approaches to studying evolution and adaptation. It begins with an overview of ways to test hypotheses about adaptive value and then sketches the ways in which information about present-day species is used to learn about phylogeny, or patterns of descent. Section 2.3 introduces a framework for thinking about how evolution shapes behavior and summarizes some of the challenges in testing comparative hypotheses about cognition. Major trends in vertebrate brain evolution, summarized in Section 2.4.1, might be expected to provide some clues about cognitive differences among major groups of animals. Indeed, some hypotheses about the causes of brain evolution are hypotheses about what brains and parts of brains allow animals to do in foraging and social life. Research on the relationship between food storing and hippocampus size in birds (Section 2.4.2) is an example of research connecting the evolution of a brain part with ecology. The debate it has occasioned about the relationship between functions and mechanisms of cognition and the brain is evaluated in the final part of the chapter.

2.1 Testing adaptation

"Drab coloration is an adaptation for reducing detection by visual predators." "Bats' sonar is an adaptation for detecting flying insects in the dark." "Reasoning ability is an adaptation to conditions in early hunter-gatherer societies." To say that some characteristic of an animal's structure, behavior, or cognition is an adaptation is to assert that it has evolved through natural selection. But selection has occurred in the past, so how can we ever test such a statement? Aren't hypotheses about adaptation no better than Kipling's *Just-So Stories* (Gould and Lewontin 1979) like "The Elephant's Child," which explains that elephants have long trunks because a hungry crocodile once stretched the nose of a curious young elephant? Perhaps just-so stories can be concocted for most situations, but in fact serious ideas about adaptation are testable using direct observation and experiment, model building, or the comparative method. In the best possible cases, all three approaches can be used in a complementary way.

2.1.1 Testing present function

A character can serve a function in the present without having been selected for that function, that is, without being an adaptation for it. Function may change over evolutionary time (Williams 1966). To take a nonevolutionary analogy, in big cities like Rome or New York one sometimes sees groups of tourists all wearing identical hats. Hats are designed (adapted) to protect the head. Originally, tour organizers may have found it convenient to give out souvenir hats that were all the same, but that having happened, the hats now serve the function of allowing members of a group to identify one another and stick together.

Evolution and present-day function are not unrelated, however. Demonstrations that a behavior serves a particular function increase confidence in the hypothesis that that function has contributed to its evolution (Cuthill 2005). A classic example of an experimental test of current function comes from Tinbergen's (Tinbergen et al. 1963) studies of eggshell removal in gulls. Soon after their eggs hatch, black-headed gulls (*Larus ridibundus*) pick up the empty eggshells, fly off, and drop them some way from the nest. Why should a bird leave its vulnerable chicks for even a few seconds to engage in this behavior? Maybe the white insides of broken shells attract predators. To test this hypothesis, Tinbergen and his colleagues distributed single gull eggs around the dunes where the black-headed gulls nest. Some of these decoy eggs had broken eggshells placed nearby; others were isolated. The eggs near broken shells disappeared sooner, eaten by crows and herring gulls, than the less conspicuous isolated eggs (Figure 2.1). Thus removing broken eggshells from the nest functions to protect offspring from the predators found where the gulls nest. This suggests a comparative hypothesis: gull species nesting in areas without this same predation pressure should not remove empty shells from their nests. Kittiwakes (*Rissa tridactyla*) provide a natural test of this hypothesis. These gulls nest on small ledges on steep cliffs, inaccessible to most predators. Kittiwakes' behavior differs from that of ground-nesting gull species in

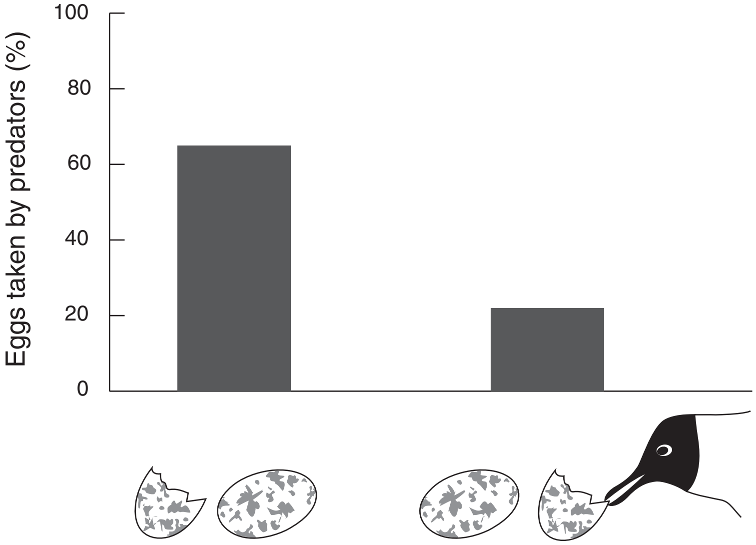

Figure 2.1. Proportion of 60 black-headed gull eggs taken by predators when the eggs were placed in the dunes near a broken eggshell (left bar) or alone, mimicking the situation in a nest from which the owner had removed broken shells (Tinbergen et al. 1963, Table 16).

several ways that can be seen as adaptations to nesting on cliffs (Cullen 1957). Among other things, they do not remove broken eggshells from their nests.

2.1.2 Adaptation as design

Many features of animals' structure and behavior seem so perfectly suited to their function that they seem unlikely to have arisen by chance. The eyes of vertebrates, the sonar of bats, the nest building and parental behavior of birds: all seem designed to accomplish their ends. Often, designs in biology are remarkably like what engineers would build to achieve the same goals. These considerations seem to compel the conclusion that intricate structures and behaviors like eyes, ears, and eggshell removal must be evolved adaptations. In pre-Darwinian days, however, such arguments from design were used as evidence for a divine creator (see Dennett 1995). Darwin's genius lay in deducing how natural causes produce the same end (Box 1.2).

A major contribution of behavioral ecology has been the use of formal optimality models to study adaptation (Chapter 11). Working out the optimal behavior for a given situation is a way of specifying the best design. One beauty of precise optimality arguments is that in principle they can be shown to be false. For example, the schooling behavior of fish had been thought to save energy for each individual by allowing it to swim in the eddies from its neighbors. However, detailed consideration of the hydrodynamics of swimming fish shows that in fact individuals of some species do not position themselves in so as to benefit as much as they could from the way the water is moved by other fish in the school. Thus, although hydrodynamic advantage may have contributed to the evolution of schooling behavior, other selective forces must have been involved (see Dawkins 1995). This is an example of how a model's predictions can fail because the modeler failed to take into account all the relevant factors. Such failures may lead to more complex models incorporating tradeoffs among competing selection pressures. In any case, evolution has not necessarily always produced the absolute optimum. Among other reasons, selection can work only on preexisting variations among individuals, including the variations thrown up by random mutations.

2.1.3 The comparative method

At most, experimental tests of function or observations of natural selection in action like the studies of Galapagos finches described in Chapter 1 can be done on only a few species. For a look at the broad sweep of evolution, at whether an important selection pressure has produced similar patterns across many species, the comparative method is essential. We have already met an informal example in the study of eggshell removal by gulls nesting in different habitats. In general, a comparative test of the adaptive value of a character consists of obtaining data from a large number of species and relating the degree to which they display the character with the degree to which the hypothesized selection pressure is present (Harvey and Pagel 1991; for an introduction see Sherry 2006). It must be applied together with good information about evolutionary relationships (i.e., *phylogeny,* Section 2.2) so similarity due to common selection pressures can be distinguished from similarity due to descent from common ancestors. Conclusions about adaptation may therefore change with changes in the amount and quality of information used to construct the associated phylogeny.

Animals live in all sorts of places and in an amazing variety of kinds of social groups. Some are solitary and cryptic except during mating. Others, like the wildebeest of the African plains or the caribou of the American Arctic, form enormous herds. Breeding may take place promiscuously, or between members of monogamous pairs or, among other possibilities, in a *polygynous* mating system, in which a few males may each control access to a harem of many females. Why have all these different social arrangements evolved? One approach to answering this question is to see if social structure can be related to ecology. Vulnerability to predators, what food a species eats and its spatial and seasonal distribution, the availability of nesting sites—all these and other variables can be related to social organization in a variety of animal groups. For example, in African ungulates, body size, habitat, group size, and mating system are related in the way shown in Table 2.1 (Jarman 1974). Smaller species need high-quality food because they have a high metabolic rate. They primarily seek fruits and buds in the forest. Because these foods are relatively sparse, the animals cannot form large groups, and there is no opportunity for one male to monopolize many females. Rather, the small-bodied forest species are found alone or in pairs. The large-bodied species graze relatively unselectively on the plains, on food that is locally very abundant but which varies seasonally in distribution with rainfall. Thus species like wildebeest tend to form large herds that migrate long distances with the seasons. Being in a group opens the opportunity for one male to monopolize several females. Hence, polygyny rather than monogamy tends to be found in the large grassland species.

Table 2.1 Relationship between ecology and social behavior in African ungulates. Reproduced from Krebs & Davies (1981); data from Jarman (1974).

	Exemplary species		Body weight (kg)			Habitat	
	Diet	Group size		Reproductive unit		Antipredator behaviors	
Group I	Dikdik Duiker	3–60	Forest	Selective browsing: fruit, buds	1 or 2	Pair	Hide
Group II	Reedbuck Gerenuk	20–80	Brush, riverine grassland	Selective browsing or grazing	2 to 12	Male with harem	Hide, flee
Group III	Gazelle Kob Impala	20–250	Riverine woodland, dry grassland	Graze or browse	2 to 100	Males territorial in breeding season	Flee, hide in herd
Group IV	Wildebeest Hartebeest	90–270	Grassland	Graze	Up to 150 (thousands on migration)	Defence of females within herd	Hide in herd, flee
Group V	Eland Buffalo	300–900	Grassland	Graze unselectively	Up to 1000	Male dominance hierarchy in herd	Mass defence against predators

By itself, especially as summarized in a paragraph, this account seems like a *Just-So Story*. Several things make it much more than that. For one, a similar account can be given of social structure in other animal groups, including birds and primates (Cuthill 2005; Danchin, Giraldeau, and Cezilly 2008). This is what would be expected if social structure is the outcome of fundamental selection pressures like the distributions of food and predators and not just associated with ecology in ungulates by chance. For another, more detailed comparative analyses have tended to uphold the conclusions from categorical analyses like that summarized in Table 2.1. Consider one correlate of social structure, sexual dimorphism in body size, that is, the degree to which males and females are different sizes (Clutton-Brock and Harvey 1984). In a variety of animal groups, males tend to be about the same size as females in species that form breeding pairs, whereas males tend to be larger than females in polygynous species. One possible explanation of this relationship is that large males have an advantage in defending females from rival males. Among primates, polygynous species may live in one-male or multi-male groups. Each male dominates more females in one-male groups. Sexual dimorphism in primates, measured as ratio of male weight to female weight, is related to mating system just as this discussion predicts (Figure 2.2).

Results like those shown in Figure 2.2 and Table 2.1 must not be distorted by unequal degrees of relatedness among the species being considered. If the species within each ecological category are more closely related to each other than they are to species in other ecological categories, differences among categories could reflect descent from a common ancestor rather than common selection pressures. One way to deal with this problem is to look at different groups of species. For instance, the same relationship between sexual dimorphism and breeding system is found in several independently evolved animal groups, suggesting that it is indeed related to the degree to which males compete for females.

Although Figure 2.2 shows a significant positive relationship between sexual dimorphism in body size and number of females per male in the breeding group, the error bars indicate that considerable variation is still unaccounted for. Correlations between characters and ecology across large numbers of species almost always use data from many sources, and inevitably some data points will represent larger numbers of more careful observations than others. However, if enough species

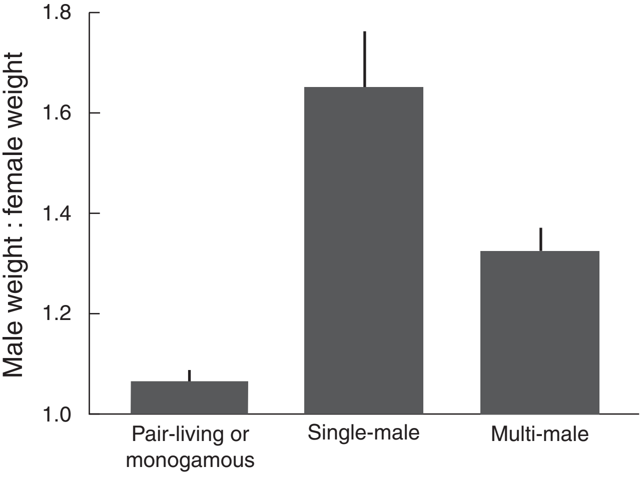

Figure 2.2. Body size dimorphism in primates, measured as the ratio of male to female body weight, as a function of whether the breeding group has a single male and female, a single male defending a group of females, or multiple males and females. Redrawn from Clutton-Brock and Harvey (1984) with permission.

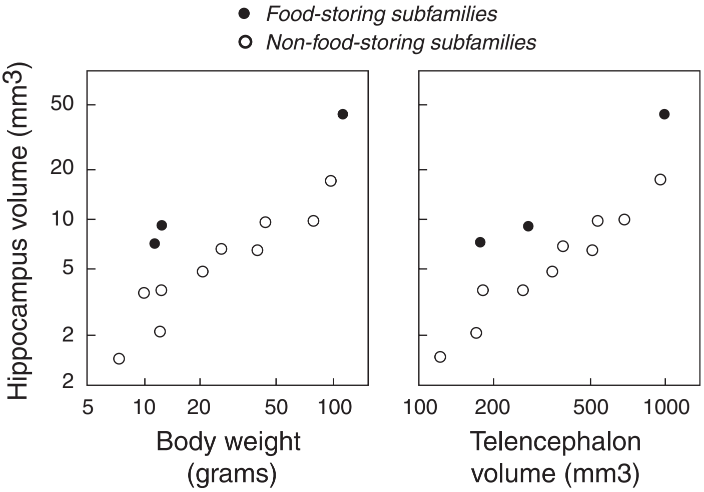

Figure 2.3. Hippocampal volume correlated with body weight (left panel) and volume of the telencephalon in birds. Redrawn from Sherry et al. (1989) with permission.

are sampled, random errors should balance each other out and genuine relationships reveal themselves. The variables examined also need to be good measures of the ecological factors being considered. For instance, ratio of females to males in the breeding group might not be the best measure of intermale competition, the factor hypothesized to favor large-bodied males, and body size is probably influenced by factors other than social structure, such as whether the animals live in trees or on the ground (Clutton-Brock and Harvey 1977).

Obvious exceptions to an overall relationship can be instructive. Figure 2.3 shows an example based on the *allometric* relationship among the sizes of body parts. Allometry refers to the principle that animals with bigger bodies have, on average, bigger body parts. A plot of the size of any structure against total body size has a characteristic slope, with most points clustered close to the overall regression line. In Figure 2.3 volume of the hippocampus, a brain structure important for memory, particularly spatial memory, in mammals and birds is plotted against body weight and against volume of the telencephalon (most of the rest of the brain) for a large number of genera of European birds. Three points stand out as being substantially above the overall regression lines indicating that three groups of birds have larger hippocampi than expected for their body and brain sizes. These all contain species that store food for the winter and retrieve it using long-lasting spatial memory. These and other data summarized in Section 2.4.2 indicate that food storing evolved together with a relatively large hippocampus.

2.2 Mapping phylogeny

Correlation is not evolutionary causation. The association between food storing and a relatively large hippocampus does not tell us about the sequence of events in evolution. Maybe food-storing species evolved an unusually large hippocampus for some unknown reason and it then allowed them to benefit from storing food. Or maybe rather than ask why some birds have such a large hippocampus relative to brain and body size we should be asking why other birds have such a small one (Deacon 1995). Such questions have to

Table 2.2

	Bird	Bat	Monkey
Wings?	Yes	Yes	No
Body Covering	Feathers	Fur	Fur
Reproduction	Lays Eggs	Live Young	Live Young
Lactates?	No	Yes	Yes

do with what ancestral species were like and how and why they changed, but suggestions of the answers to them can be found by looking at present-day species, given some reasonable assumptions about how evolution works. This is the study of phylogeny, or the reconstruction of the tree of life, the branching relationships among species during evolution (Stearns and Hoekstra 2005).

Suppose we have a bat, a bird, and a monkey. The bat is like the bird in having wings, but it is like the monkey in having fur instead of feathers, lactating, and giving birth to live young instead of laying eggs (Table 2.2). On the basis of these four characters, we would classify bats as more closely related to monkeys—that is, having a more recent common ancestor—than to birds because bats and monkeys have more characters in common. Moreover, although bats and birds both have wings, they differ embryologically and in details of structure. Thus they are *homoplasies* (or *analogies*), not *homologies,* that is, they have evolved from different ancestors and converged on a similar shape due to common selection pressures of an aerial way of life rather than being descended from a common winged ancestor. Differences between the bat's limbs and the monkey's reflect a third evolutionary outcome, *divergence* from a comparatively recent common (mammalian) ancestor (for further discussion see Papini 2002; Papini 2008).

Biological classification is hierarchical. Figure 2.4 shows three ways of representing the nested relationships among species. A phylogenetic tree represents the divergence among species over time. The times at which species diverged from an ancestral state can be tied down by examining the fossil record and/or from molecular evidence based on species differences in DNA and/or other molecules and assumptions about the rate of random mutation of DNA. Figure 2.5 shows the phylogeny of primates

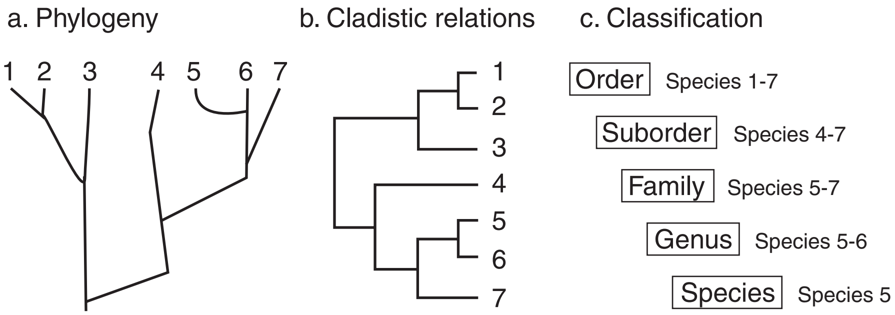

Figure 2.4. For seven fictitious species, the relationship between a phylogenetic tree (divergence as a function of time), a cladistic classification, and—for species 5—the traditional classification in terms of species, genus, and so forth. As an example of how to read panel b, species 1 and 2 share a character they do not share with species 3, while all three of them share a character not shared with species 4–7. Redrawn from Ridley (1993) with permission.

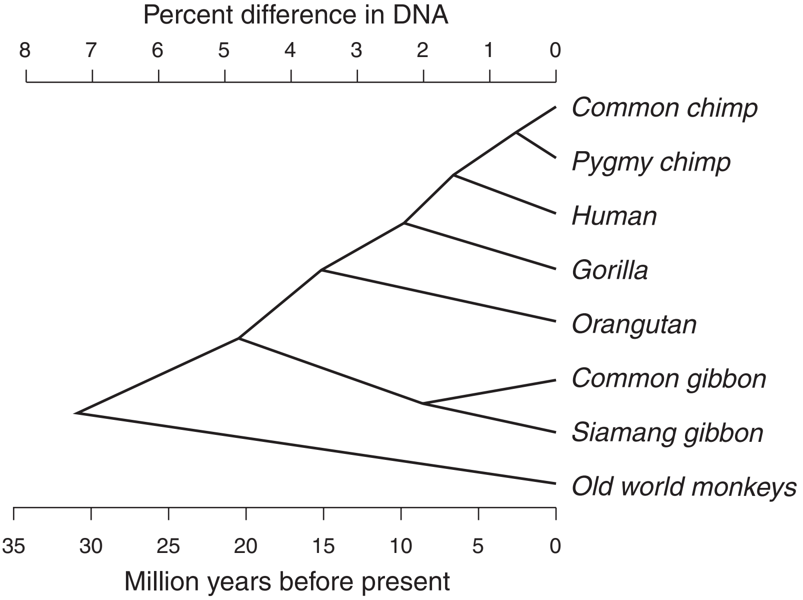

Figure 2.5. Phylogenetic relationships of old-world monkeys, apes, and humans as revealed by DNA hybridization. Greater similarity in DNA (top axis) indicates more recent divergence (bottom axis). Redrawn from Ridley (1993) with permission.

based on molecular evidence. Many diagrams of primate phylogenies betray our continuing belief that humans are the "highest" primates by putting them at the top (Hodos and Campbell 1969; Nee 2005). In fact, the arrangement of species branching from a particular node is largely arbitrary. What matters is the nodes (i.e., connections), not which ones are higher on the page or further to the right or left. Figure 2.5 puts chimpanzees at the top to emphasize the sequence in which the species diverged from common ancestors.

The classification of organisms into *clades,* or groups descended from a common ancestor, can be based on characters of present-day species alone. Nowadays an important part of this process is comparison of gene sequences and proteins and use of sophisticated statistical techniques that take into account large numbers of characters (see Pagel 1999). But the simple example in Table 2.2 is enough to show the logic of phylogenetic reconstruction. Without knowing anything about genes or the fossil record, we could infer from the table that bats and monkeys share an ancestor that had fur, gave birth to live young and lactated (i.e., a mammalian ancestor) that was not ancestral to birds. Such inferences rely on the notion that any particular evolutionary change is improbable. For a new species to evolve, an advantageous rather than a deleterious or lethal mutation has to occur and spread. It is therefore more likely that shared characteristics were present in a common ancestor than that they evolved several times independently. Representations of cladistic classification can display the characters that have changed as species diverged, as in Figure 2.6. Finally, although the classification of organisms into species, genera, families, and so on is also hierarchical, traditional classifications of species groups do not always correspond so closely to the other classifications as in Figure 2.4c.

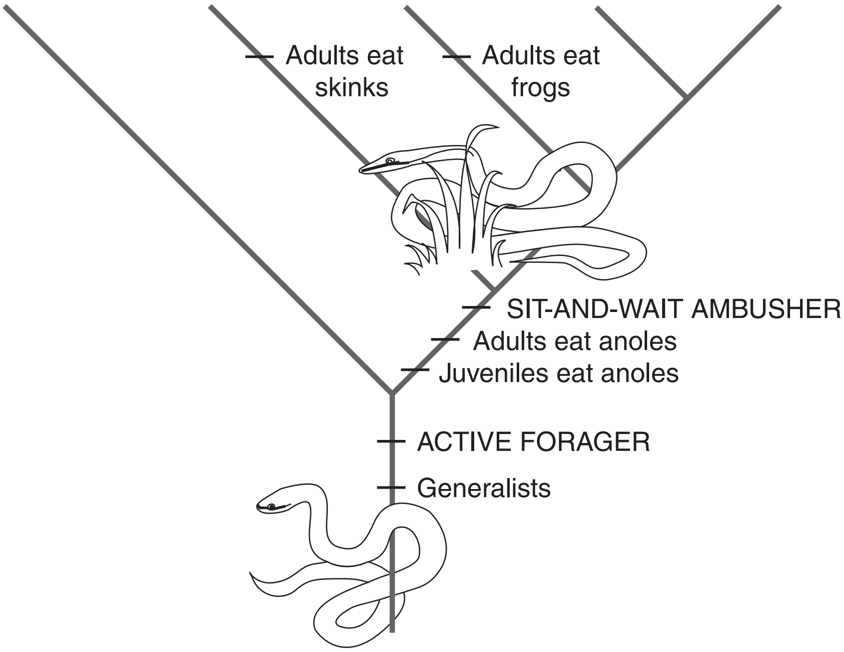

Figure 2.6. Cladogram for colubrid snakes on the island of Hispanola based on their feeding behavior. The species of interest (the four rightmost branches) and a comparison group of close relatives (the outgroup, left branch) all evolved from active generalist foragers. Evolutionary changes inferred from shared characters are indicated along the branches. Time is not explicitly represented in this type of diagram, unlike that in Figure 2.5. Redrawn from Brooks and McLennan (1991) with permission.

2.3 Evolution, cognition, and the structure of behavior

Studying cognition entails inferring mental organization from observing behavior, but behavior reflects sensory, motor, and motivational as well as cognitive mechanisms. This section introduces a general framework for thinking about the organization of behavior which is useful for thinking about how evolution affects behavior and cognition.

2.3.1 Behavior systems

Behavior is organized into functional systems like hunger, fear, and sexual behavior, called *instincts* by Tinbergen and other classical ethologists. These are hierarchical organizations of motor patterns that share some proximate causal factors (Timberlake 1994; Hogan 1994b). For example, an animal's hunger system includes the behavior patterns that change in frequency, intensity, or probability when it has been deprived of food and/or is in the presence of food. For a chicken, these might be walking around, scratching the ground, and pecking. A behavior system also includes relevant stimulus processing (perceptual) mechanisms and central mechanisms that coordinate external and internal inputs (Figure 2.7). In the case of the hunger system in a chicken, a central motivational mechanism integrates the bird's state of depletion or satiation with visual information to determine whether or not it will peck at what it

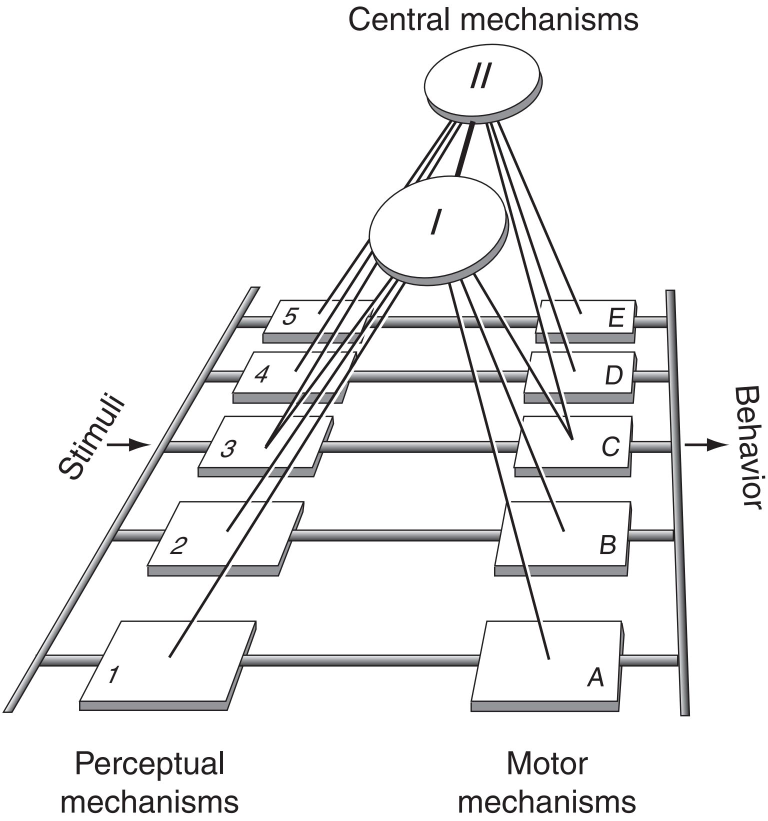

Figure 2.7. The structure of behavior systems. Stimuli are processed by perceptual mechanisms (1–5) and may affect motor mechanisms directly, as in reflexes (horizontal lines) or through the mediation of central mechanisms, of which two (I and II) are indicated. Each interconnected set of perceptual, central, and motor mechanisms forms a behavior system, so two behavior systems are shown here. Some motor mechanisms, such as C, which might be walking or pecking, may belong to more than one behavior system. Redrawn from Hogan (1988) with permission.

sees (Hogan 1994b). Cognitive mechanisms are part of this organization, too. Whether the chicken pecks at the thing in front of it may be influenced by what it is attending to and by past learning about the consequences of pecking.

As just described, behavior systems are defined causally (Hogan 1994b), in terms of internal and external causal factors rather than immediate outcome or apparent goal. However, the causal organization of behavior must make functional sense. An animal that ignored food while starving or approached predators rather than hiding or running away would be unlikely to have as many offspring as one that ate when hungry and fled from danger. Animals that ignore food when deprived or behave in a friendly manner toward predators have been weeded out by natural selection not because they are "too stupid" to forsee the dire consequences of their acts but because they leave fewer copies of their genes than do individuals whose motivational and cognitive mechanisms result—blindly—in their being better-nourished and less preyed upon. This relationship is depicted in Figure 2.8. Natural selection shapes cognition in an indirect way. Cognition—processing environmental information—results in behavior. That behavior has an immediate consequence such as ingesting

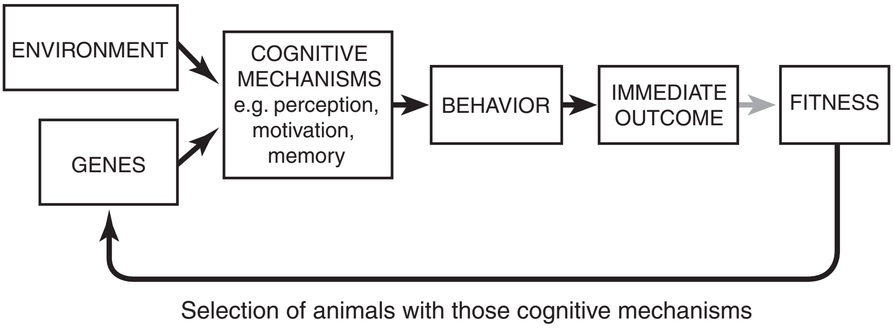

Figure 2.8. How cognition and behavior are shaped by natural selection. Adapted from Shettleworth (1987) with permission.

food, depositing sperm in a fertile female, strengthening a nest. In the long run, such consequences have a measurable impact on the individual's fitness and thereby on the representation of genes contributing to development of the mechanisms that generate that behavior.

With few exceptions, like nest-building and burrowing, behavior does not leave fossils. But the evolution of behavior can nevertheless be inferred from phylogeny, as indicated in Figure 2.6. In terms of the organization of behavior systems shown in Figure 2.7, species differences could evolve in sensory, motor, or central mechanisms. For instance, the range of energies detectable by the senses could expand or contract, new motor patterns could appear, and/or the central coordination of input and output could change. The evolution of behavior can be traced at a more detailed level, too. For instance, species differences in motor patterns may be analyzed into differences in muscular and skeletal anatomy and patterns of firing in nerve cells (Lauder and Reilly 1996). Species differences in visual sensitivity related to differences in the kind of light prevalent in different environments might be related to differences in photopigments and the genes for producing them (see Chapter 3).

The loss of bat-avoidance behavior by moths on Tahiti is an example of evolutionary change nicely accommodated by this way of thinking about behavior. The raison d'être for hearing in most moths is to avoid bats, which search for moths in the dark using ultrasonic cries. Accordingly, a moth's simple auditory system is tuned to ultrasonic frequencies because moths can avoid bats by dropping immediately to the ground when they hear one. Although bats have apparently never been present on the Pacific island of Tahiti, the auditory nerves of the moth species that arrived on Tahiti millions of years ago (*endemic* species) still fire to bat cries. Nevertheless, when bat cries were played to endemics in flight, they did not drop to the ground like individuals of more recently arrived species. Assuming that the endemics are still capable of altering their flight in response to other stimuli, this pattern of findings indicates that in the absence of selection the sensory input has been decoupled from the motor avoidance response (Fullard, Ratcliffe, and Soutar 2004).

Many morphological (i.e., structural) differences among species result from relatively small changes in developmental programs, that is, from changes in when specific genes are turned on and off (see Stearns and Hoekstra 2005). A speeding up or slowing down of growth in one part relative to others can result in dramatic

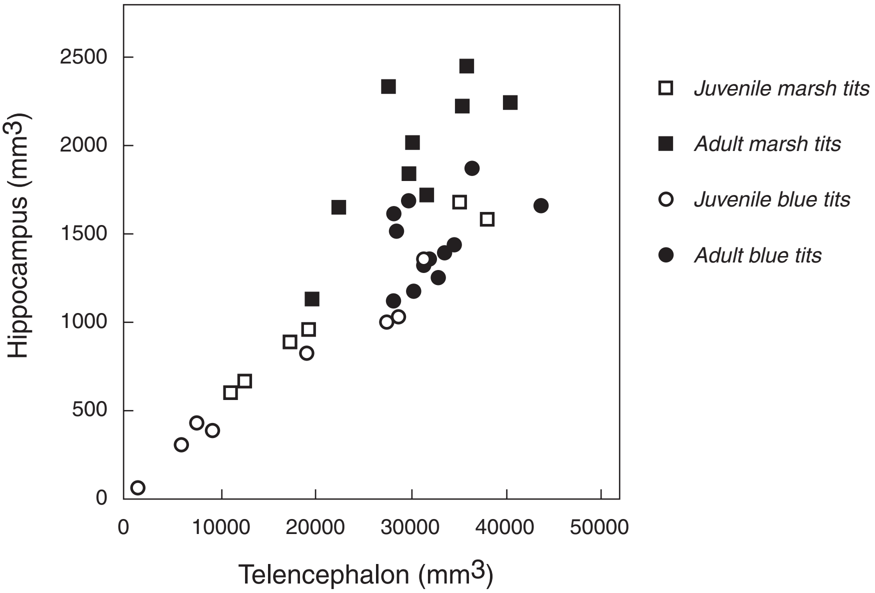

Figure 2.9. Growth of hippocampus and telencephalon (most of the rest of the brain) in marsh tits, a food-storing species, and blue tits, which do not store food. Redrawn from Healy, Clayton, and Krebs (1994) with permission.

changes in shape. The brains of food-storing birds provide one example related to cognition (Figure 2.9). In baby marsh tits (food-storers) and baby blue tits (nonstorers), the whole brain grows rapidly in the first few weeks after hatching. At this stage, the hippocampus develops relative to the rest of the brain in the same way in both species. By around 6 weeks after hatching, when the babies are feeding themselves and the marsh tits are starting to store food, brain growth has slowed down. However, the marsh tits' hippocampus continues to grow, so that the typical food-storers' larger hippocampal size relative to the rest of the brain appears by the time memory for storage sites is needed (Healy, Clayton, and Krebs 1994). Magpies (food-storing corvides and jackdaws (nonstoring corvids) show the same pattern (Healy and Krebs 1993). In the case of marsh tits, experience using spatial memory also contributes to the species difference in hippocampus, but blue tits are not influenced by experience in the same way as marsh tits (Clayton 1995).

Darwin was deeply impressed by how behavior as well as structure could be artificially selected by animal breeders. And in *The Origin of Species* he speculated on how complex and intricate behaviors like the comb-building behaviors of honey bees could have evolved in small steps. Nowadays, genetic engineering can be used to demonstrate that particular genes contribute to particular behaviors or cognitive processes and to analyze the mechanisms by which they do so (Mayford, Abel, and Kandel 1995; Fitzpatrick et al. 2005). Natural selection can provide molecular geneticists with opportunities to dissect how genetic changes have produced species differences, including differences in cognition and behavior. Bringing together information derived from genetic engineering with phylogenies of real species offers exciting possibilities for research on the mechanisms of evolutionary change (see Fitzpatrick et al. 2005; Grant and Grant 2008).

2.3.2 Evolution and cognition

Most tests of adaptation mentioned in Section 2.1 involve comparing different species or groups of species: ground-nesting vs. cliff-nesting gulls, solitary vs. social species of ungulates, and so on. Naturally, any such comparison must be done carefully. For example, when correlating social group size and male body size, it is important to be sure the values going into the analysis are representative of the species and to take account of other variables that might be confounded with the variables of interest. Comparing cognition across species encounters its own particular difficulties, which largely arise from the fact that behavior is influenced by a host of processes that are not specifically cognitive. As a result, conclusions like "species A has more of ability X than species B" always need to be viewed critically. The same is true in comparisons of genetically manipulated animals. This section introduces some of the general problems in doing comparative research on cognition, taking as an example research on male-female differences in spatial memory in different species of rodents. This is not to imply that such problems have not been addressed in this area; as we will see, many have been dealt with rather well.

In many monogamous animals, the male and female occupy a territory together, whereas in some polygynous species females have relatively small territories where they rear their young, while males range over larger areas, visiting several different females for mating. These observations suggest that in monogamous species males and females need similar abilities to find their way around and remember the locations of resources in the pair's territory, whereas in polygynous species males need a better-developed ability to process and remember spatial information than do females. This hypothesis about the relationship between spatial cognition and mating system has inspired research on sex differences in brain and spatial cognition in several groups of rodents (Gaulin 1995; Jacobs 1995; Sherry 2006). It is arguably the most coherent and best-supported of several proposed evolutionary explanations for the sex differences in spatial cognition observed in a variety of mammals, including humans (see Jones, Braithwaite, and Healy 2003).

The specific hypothesis here is that males and females do not differ in spatial ability in monogamous species whereas there is a difference in favor of males in polygynous species. But to evaluate it, we cannot necessarily just test males and females of a number of different species all in the same way because a test standardized in terms of physical variables may affect different species differently. For instance, animals that become frightened and stay close to the walls in a big open space might take longer than bolder animals to learn to swim straight to the dry platform in the middle of a pool of water. Recent research on animal personality (Box 2.1) has provided plenty of evidence for stable within- and between-species differences in behavior that could influence the outcome of cognitive tests as this example suggests. If the animals are rewarded with food, we need to be sure all species are equally hungry and equally fond of the reward provided. If we compare them on discrimination learning, we need to know that they process the stimuli involved in the same way, that is, we need to know something about their sensory systems. Such considerations underline the importance of what Macphail (1982, 1987) called *contextual variables*. Within any species, many aspects of the experimental context, some much less obvious than timidity or reward size, can affect what animals do. Therefore, any species difference on a single task could reflect different effects of contextual variables on performance rather than the cognitive ability that performance is supposed to measure.

Box 2.1 Animal Personality?

Anyone who has had pets will know that animals seem to differ in characteristics such as boldness, aggressiveness, and sociability. In people these would be referred to as personality traits. For nonhuman species the term *behavioral syndromes* (Sih et al. 2004; Bell 2007) is often used to refer to the analogous observation that suites of related behaviors seem to vary together across individuals. In one very well studied case, for instance, wild great tits (*Parus major*) that are quickest to move through a novel environment tend to be quickest to explore a novel object and most aggressive toward conspecifics (Dingemanse and Reale 2005). In effect, human personality is also measured by behavior, even if only on paper-and-pencil tests, so *animal personality* (Dingemanse and Reale 2005) or *temperament* (Reale et al. 2007) is increasingly used in this comparatively new area of research in behavioral ecology. Candidates for behavioral evidence of a given characteristic such as boldness, aggressiveness, or sociability must be repeatable within tests of the same individual and correlated across related tests. Validating tests of animal personality is not always easy or straightforward, and methods for doing so are still debated (Miller, Garner, and Mench 2006). Nevertheless, with great tits and a few other species there is considerable evidence both that individual differences are heritable and that they show up in both behavior and reproductive success in the wild (Dingemanse and Reale 2005).

The existence of cross-situational individual differences in behaviors with fitness consequences creates difficulties for evolutionary models that assume all individuals exhibit the same range of variation in behavior. Strong personality traits might be maladaptive. For instance, an animal that is consistently shy may fail to discover new resources being exploited by its bolder conspecifics. How can two or more behavioral syndromes coexist in a species or population and why do they take the form they do? For example, why is boldness vs. shyness a dimension of individual difference in so many species? One proposal (Wolf et al. 2007) is that many aspects of animal personality represent a fundamental tradeoff between risk-seeking and risk-avoiding life history strategies. A bold, quick, aggressive approach to life can increase fitness by permitting early reproduction but it is also dangerous; less bold and risky behaviors delay reproduction, but they may have an advantage when conditions are relatively stable or when there will be more opportunities for reproduction in the future (i.e., when the time horizon is long). When the environment varies on an appropriate scale, both risk-seeking and risk-avoiding personality types can persist because either one can be successful depending on circumstances (Dingemanse and Reale 2005; Wolf et al. 2007).

Research on animal personality has implications for comparative research on cognition because many of the differences that have been documented among individuals, populations, or species involve behaviors that often play a role in cognitive tests. One obvious example is that because willingness to move around in a novel environment and explore the things in it is a prerequisite for many traditional tests of learning, boldness or tendency to explore may predict fast acquisition of new tasks even though it is not necessarily correlated with learning ability as such. As another example, fearfulness (Miller et al. 2006) might be positively correlated with speed of acquisition in an avoidance task, but negatively correlated in a maze-learning task. Attempts to test general learning ability, or animal IQ (if there is such a thing), have controlled for such motivational or behavioral predispositions by using a variety of tasks, as done by Matzel and colleagues with mice (Matzel et al. 2003).

One proposed solution to this problem is *systematic variation* (Bitterman 1965). This means testing the animals under several values of relevant contextual variables. For instance, the difficulty of the task should be varied over a wide range. Gaulin and Fitzgerald (1989) did just that by using seven different mazes to compare spatial learning in monogamous prairie voles (*Microtus ochorogaster*) and polygynous meadow voles (*M. pennsylvanicus*). Meadow vole males performed better than meadow vole females on all the mazes, but, as predicted, there was no sex difference in the prairie voles (Figure 2.10). Importantly, the mazes seem to be a fair test of species differences in that both species score about the same on average on any given maze. They are also not so hard that most animals fail or so easy that everyone does perfectly, which is important because “floor” or “ceiling” effects, respectively, could obscure group differences.

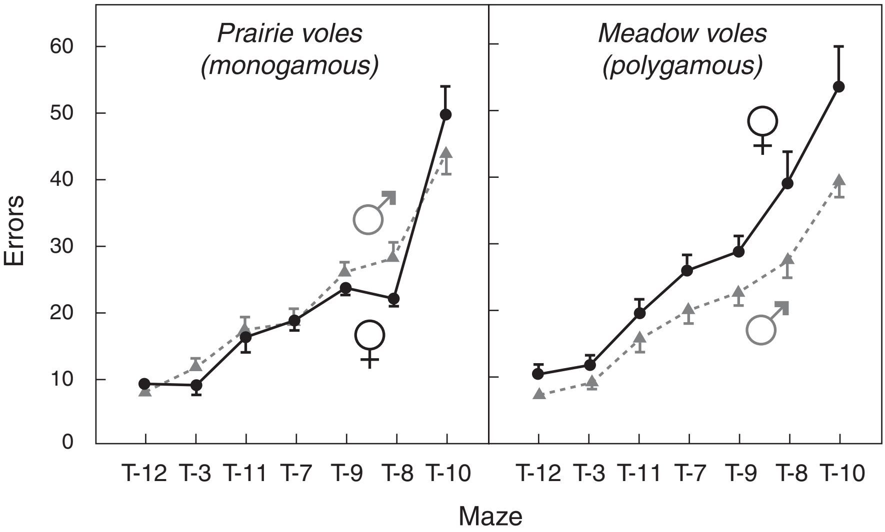

Figure 2.10. Number of errors made by male and female voles of two species in a series of increasingly difficult mazes. Data from Gaulin and Fitzgerald (1989) redrawn from Gaulin (1995) with permission.

Systematic variation has two sides. In cases like that originally discussed by Bitterman (1965), one species fails to show some effect shown by another or shows it to a much smaller degree. Clearly, if it is already known that the strength of this effect in species that show it is influenced by some contextual variable, then this same variable should be manipulated with the second species to be sure it was not just at an unfavorable level initially. Here, systematic variation amounts to trying to reject the null hypothesis that no factor other than differences in cognition is responsible for differences in performance (Kamil 1988). To return to our case study, it might be suggested that sex differences in activity are responsible for sex differences in performance in spatial tasks. This possibility has been rendered implausible by showing that males' and females' activity levels are similar under a range of conditions (Gaulin, FitzGerald, and Wartell 1990). But a skeptic might then suggest another confounding factor, further systematic variation would have to be done, and so on ad infinitum. Kamil's proposed solution to this problem is, instead of systematically varying factors within a given task, to vary the tasks. For instance, if food-storing and nonstoring species differ in ability to process and remember spatial information, these differences ought to be detectable in a variety of different spatial tasks. There may of course be tasks or species for which contextual variables are overwhelmingly important, but if enough tasks are used, the results should converge on a single conclusion. Kamil and his colleagues have used this approach with considerable success to compare memory for spatial information in food-storing vs. nonstoring species of birds (Box 1.4; Chapter 7).

The other side of systematic variation is emphasized by Papini (2008): if an independent variable affects species in the same way, even if their levels of performance generally differ quantitatively, this is evidence for a shared process. Figure 2.10 provides an example. Although male meadow voles perform better than females, their errors still increase with maze complexity. Systematic variation appears frequently throughout this book as a way to discover whether very different species, exhibiting behaviors as different as speaking vs. pressing a key vs. digging up a worm, have access to the same kinds of cognitive processes. The tests of blindsight in monkeys described in Box 1.1 are an example. This approach is also, as in Chapter 7, referred to as testing for functional similarity. Most importantly, examples of what can be learned from systematic variation underline the principle that conclusions about species differences in cognition must always be based on more than a single test.

Ideally, a thorough comparative test of an ecological hypothesis includes tests on which the species are predicted not to differ, or—even better—to differ in the opposite direction. Such tests can help to rule out the possibility that one group performs better than another because of some general factor like how well they adjust to the lab. In food-storing species of corvids (the crow family, including jays and nutcrackers; Box 1.4), some species are highly social while others are not. Therefore, the pattern of species differences in social cognition may differ from that in spatial cognition (Balda and Kamil 2006). Sex differences in spatial behavior related to space use in the wild may be present only in the breeding season (Galea et al. 1994; Sherry 2006). Such seasonal or developmental changes within individuals of the same species offer excellent opportunities for testing adaptive relationships among cognition, brain, and natural behavior with minimal confounds from contextual variables. An example is the comparison of spatial and other kinds of memory in white-footed mice exposed to summerlike vs. winterlike photoperiods (Pyter, Reader, and Nelson 2005). However, even comparisons within a species may be subject to motivational or other confounds. For example, the time available for feeding may differ when animals live in days of different lengths, and/or the animals in short days may reduce their activity or metabolic rate.

A general problem with applying the comparative method to behavior and cognition is getting enough independent comparisons. One solution to the practical difficulties of testing large numbers of species is to build up a sample gradually by comparing two species at a time, in this case one monogamous species with one closely related polygynous species, but we need to be able to find a sufficient number of lineages in which monogamy arose separately. Research relating spatial ability to mating systems has been done on, among other rodents, voles (*Microtus*) and mice (*Peromyscus*), and of course the hypothesis could also be tested on birds with appropriate mating systems (Jones, Braithwaite, and Healy 2003).

Exceptional spatial ability may be associated with other exceptional demands on spatial learning and/or memory in the wild. For instance, birds that migrate might be expected to use memory and spatial learning more than relatively sedentary populations, not necessarily because they actually need learning to migrate, but because they need to acquire spatial and other information about each of the places where they spend a few months at the ends of their travels, and perhaps at stopovers along the way. They might also form long-term memories for the areas where they regularly spend part of the year, so as not to waste time relearning their stable features. There is some evidence consistent with this hypothesis (e.g., Cristol et al. 2003; Mettke-Hofmann and Gwinner 2003). Not only amount but kind of spatial learning might be expected to be associated with different ecological demands. For example, individuals living in different kinds of habitats might rely on different kinds of spatial cues. In one test of this notion, Odling-Smee and Braithwaite (2003) found that stickleback fish from ponds relied more on landmarks than fish of the same species from fast-moving streams.

2.4 Evolution and the brain

2.4.1 Patterns of vertebrate brain evolution

To look for patterns in a large sample of species, it is a lot easier to measure brains than to measure behavior and infer cognitive structures. As a result, compared to what we know about the distribution of any cognitive ability across the animal kingdom, we know vastly more about the brain, at least in vertebrates. Figure 2.11 shows the relationship of brain weight to body weight in the major groups of vertebrates. The polygons enclosing data from each taxonomic group (*taxon*) indicate that brain size can vary considerably even for animals of a given group with a given body weight, as illustrated for mammals in teh lower panel of Figure 2.11. There is a trend for larger brains during vertebrate evolution. For instance, birds are thought to have evolved from a primitive reptile, and the polygon for birds is entirely above that for reptiles, indicating that in general birds have larger brains than reptiles of equivalent size. On the whole, mammals have the largest brains for their body weight, but small mammals overlap considerably with birds. Within mammals, humans are the species farthest in perpendicular distance above the group regression line (details of each taxon in Chapter 4 of Striedter 2005).

Within a lineage, why do some species have larger brains relative to their body weights than others? Brains are metabolically costly to maintain (Laughlin 2001), so there must be some advantage to having a large brain. Not surprisingly, hypotheses about the function of relatively large brains have focused on the assumed connection between brains and cognitive abilities. For instance, the “foraging intelligence hypothesis” of primate brain size proposes that fruit-eating species need excellent spatial and temporal learning abilities for tracking the locations and ripeness of items that are scattered widely throughout the forest whereas leaf eaters do not need such abilities. The “social intelligence hypothesis” (Chapter 12) suggests that animals living in large groups in which individuals have differentiated and ever-changing social roles need to keep track of the identities of large numbers of individuals and their interactions. Tests of the various versions of these hypotheses have relied on comparative studies relating primates’ brain size to proxies for cognitive abilities such as type of foraging niche or social group size (review in van Schaik and Deaner 2003; Healy and Rowe 2007).

Among birds, parrots and corvids have the biggest brains for their body sizes. As we will see, some corvids may have social and tool-using abilities comparable to those of some primates. These, along with relatively large brains, appear to represent convergent evolution in separate vertebrate lineages (Emery and Clayton 2004). Relatively new are the comparative studies of primates and birds described in Box 2.2 indicating that brain size is related to propensity for innovation. To the extent that foraging on ephemeral food sources, managing social relations, and acquiring novel behaviors call on common abilities, these explanations for the evolution of large brains need not be mutually exclusive (Striedter 2005). In any case, most accounts of relative brain size in terms of complex behaviors are still largely speculative pending more direct evidence about the neural substrates of the behaviors in question (Healy and Rowe 2007).

The foregoing discussion addresses the whole brain, but the relationship of relative hippocampus size to food-storing in birds depicted in Figure 2.3 suggests that maybe we should be looking at how individual parts of the brain evolve in association with specific behaviors or ecological variables. Whether brain

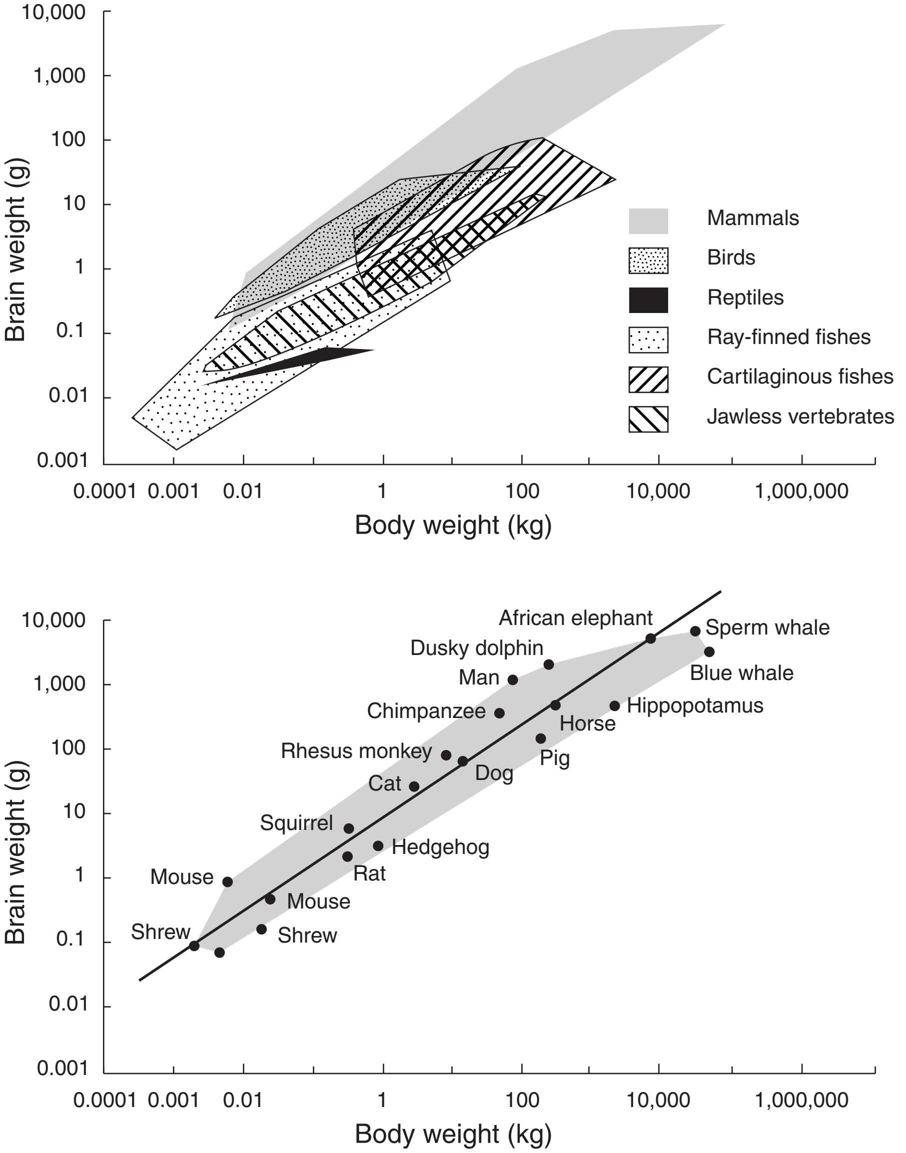

Figure 2.11. Relationships between overall brain weight and body weight in vertebrates, on logarithmic scales. Top panel: data for major groups as the minimal polygon which encloses each one's data. Redrawn from Striedter (2005) with permission. Lower panel: data for selected species of mammals surrounded by its minimal polygon. The dark slanted line is the overall regression line for mammals. The perpendicular distance of a species' data from this line (formally, the *residual*) is a measure of how much it deviates from the average allometric relationship for mammals. Redrawn from Roth and Dicke (2005) with permission.

evolution is *concerted* or *mosaic*, that is, whether brain size evolves as a whole or through selection on particular parts, is a contentious question in comparative neuroanatomy (see discussions accompanying Finlay, Darlington, and Nicastro 2001 and Striedter 2006). Figure 2.11 is consistent with concerted evolution because it shows an evolutionary trend toward larger brains.

Box 2.2 Innovation and the Brain: General Intelligence after All?

About ten years ago, Louis Lefebvre and colleagues (Lefebvre et al. 1997; reviews in Reader and Laland 2003; Lefebvre, Reader, and Sol 2004) suggested that the limitations of laboratory studies for obtaining data on cognition in large numbers of species could be overcome by looking at the many reports of innovative behavior in natural history journals. Such innovations usually take the form of foraging behaviors described as novel or unusual for the species, such as eating a new food or using a new foraging technique. For example, magpies might be seen digging up potatoes (Lefebvre et al. 1997). Raw frequencies of such reports can be corrected for obvious biases such the general rate of publication on those species and then combined for groups of species, correcting for number of species per group, to get a measure of innovation rate for, for example, all corvids, parrots, or pigeons (see Figure B2.2 for details). This measure of "intelligence" in the field correlates with available data on learning in the same species in the laboratory (Lefebvre, Reader, and Sol 2004). An alternative approach (Ramsey, Bastian, and van Schaik 2007) is to infer that innovation must have occurred when populations of a species differ in ways that cannot be ascribed to local ecological factors (cf. discussion of animal cultures in Section 13.5). Either way, an innovation is a *product* of some unidentified behavioral process(es). These processes are generally assumed to be similar to those that contribute to human intelligence or inventiveness.

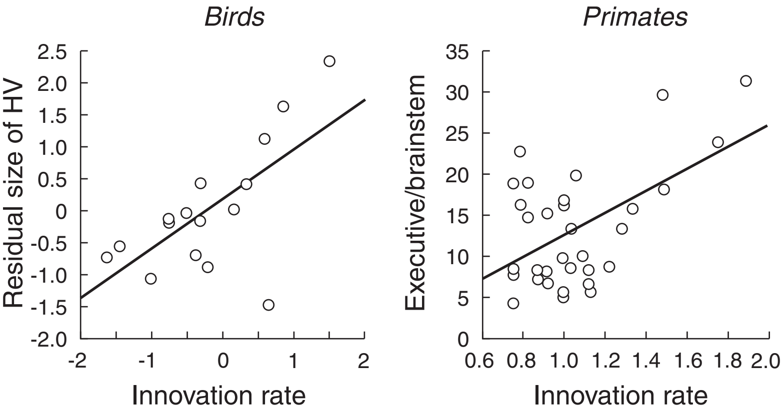

Figure B2.2. Relationship between size of parts of the brain and innovation. For birds (left), residuals (see Figure 2.11) are used as a relative measure of both innovation rate and size of the neostriatum plus hyperstriatum ventrale (HV), areas involved in learning. For primates (right) the "executive brain" (see text) is measured relative to volume of the brainstem. Innovation rates are based on the number of innovations reported for a species relative to overall number of articles about that species (details in Reader and Laland 2002). Redrawn from Lefebvre, Reader, and Sol (2004) with permission.

Analysis of hundreds of reports of innovative feeding behaviors in birds shows that rate of innovation in a bird order is correlated with overall size of the brain and with size of the forebrain (Figure B2.2). Innovation rate is potentially significant for evolution because it also predicts whether a species will become established when introduced into a new environment (Sol et al. 2005). Data from primates examined in a similar way also show a positive relationship between innovation rate, as well as tool using and social learning frequency, and "executive brain ratio" (volume of the forebrain and striatum relative to the brainstem, Figure B2.2; Reader and Laland 2002; see also Reader and Laland 2003). The association of innovation or general behavioral plasticity with overall brain size seems more consistent with the old assumption (Chapter 1) that animals have a "general intelligence" than with the idea that cognition and the brain are largely modular (Box 2.3; Lefebvre and Bolhuis 2003). These ideas are not necessarily incompatible. For humans, it has been suggested that IQ measures a flexibility needed for dealing with evolutionarily novel situations that is not afforded by coexisting modular systems (Kanazawa 2004).

Innovation may be related to overall brain size precisely because innovative behavior is a heterogeneous category any instance of which involves one or more of a concatenation of factors. Indeed, large brain areas such as forebrain that are associated with innovation rate are involved in multiple behaviors (Sherry 2006; Healy and Rowe 2007). For example, to profit from a chance encounter with a new way of getting food, it helps to be able to learn quickly, presumably using a rather general ability to associate events and their consequences. But to do something new in the first place, especially if that requires interacting with a new object, food, or location, it helps to be not too neophobic, and in fact Webster and Lefebvre (2001) showed in a series of laboratory and field tests that of the species of birds they studied, those rated as most innovative were indeed least neophobic. Thus part of innovativeness may be general boldness, perhaps an aspect of personality (Box 2.1), rather than cognitive ability per se. Similarly, general mechanisms of reinforcement may explain why innovative feeding behaviors may persist and spread when food is scarce. For these sorts of reasons, it seems unlikely that innovations are the products of a single specialized cognitive process.

Historically, brain evolution was thought to be a matter of adding new, more advanced, structures to primitive ones in a linear fashion leading up to primates and humans. Hence the prevalence of prefixes such as “paleo,” “neo,” and “archeo” to label structures in traditional brain anatomy. It is now recognized that all vertebrate brains have the same basic parts, although their relative sizes and detailed structures are characteristic of each vertebrate group (Avian Brain Nomenclature Consortium 2005). Within a lineage, larger brains are not just scaled up versions of smaller ones. Bigger brains need a more modular organization (Box 2.3), and this well might lead to cognitive differences between big- and small-brained species within a group, for example, primates vs. rodents or parrots vs. canaries. The proportion of the brain occupied by particular structures such as the neocortex also tends to differ in a systematic way in larger-brained species, apparently consistent with mosaic evolution. However, on one theory (Finlay, Darlington, and Nicastro 2001) most of this variation is consistent with concerted evolution because it reflects the way in which common processes of very early brain development produce larger brains. Indeed, a recent survey (Striedter 2005) finds that the majority of the evidence is consistent with concerted evolution in that within a given taxon, and after taking into account developmental constraints, the relative size of a given structure generally does not show very dramatic deviations across species. “Not very dramatic” means not more that about a 2- or 3-fold difference in size relative to the rest of the brain. Within this context, the hippocampus–food storing story is “wonderful” (Striedter 2005, 173) as a potential example of at least mildly mosaic evolution. It is also an instructive case study of the challenges of trying to connect brain, behavior, and cognition in a rigorous way.

2.4.2 Hippocampus and food storing in birds

The *principle of proper mass* (Jerison 1973) as a tenet of comparative neuroanatomy says that the more important a function is for a species, the more brain area will be devoted to it. This principle is most sensibly interpreted as applying to the size of a structure relative to other parts of the brain in comparisons of reasonably close relatives (Striedter 2005). Sensory and motor areas provide some spectacular

Box 2.3 Modularity in Development, Evolution, and Cognitive Science

Anyone who has written a computer program or assembled a chest of drawers from IKEA is acquainted with modularity. Modularity, or organization as somewhat independently functioning but interconnected subunits, is a fundamental aspect of complex systems (Simon 1962). Indeed, Simon (1962) argued vividly that complex systems cannot develop or function effectively unless they consist of a hierarchical organization of parts. Not surprisingly then, it has been claimed that modularity "is a universal property of living things and a fundamental determinant of how they evolve." (West-Eberhard 2003, 56 ; see also Schlosser and Wagner 2004). Hogan's (1994a) definition of a behavior system (Section 2.3.1) as a "set of sensory, motor and central mechanisms that function as a unit in some situations" could be taken to suggest that animal behavior as a whole is modular, and indeed, the discussion by West-Eberhard just cited goes on to include modularity of behavior and to connect modularity at all levels to fundamental processes in development. In turn, developmental modules may function as basic units of evolution (Schlosser and Wagner 2004; Callebaut and Rasskin-Gutman 2005).

Notwithstanding its status as a basic feature of biological systems, *modularity* is fraught with debate and disagreement in cognitive science. Most of this centers on the properties of "the modularity of mind" proposed by Jerry Fodor (1983) in his book of the same name (Barrett and Kurzban 2006). In Fodor's sense, a module is among other things an informationally encapsulated perceptual system: it acts exclusively on a restricted kind of input unconsciously but in an apparently intelligent way. What this means is illustrated in a simple way by the Muller-Lyer illusion (Figure B2.3). The upper line appears longer than the lower one, presumably because some feature of the drawing is a trigger (Gigerenzer 1997) for a visual perceptual system that makes implicit inferences about the relative sizes and distances of objects. *Encapsulation* refers to the fact that the system is impenetrable to information from other systems, in this case the "higher level" information obtained from measurement: measuring the lines and discovering that they are equal does not abolish the illusion. Modules are *domain specific* in that the computations or "rules of operation" (Sherry and Schacter 1987) implicit in the output of a particular module are applied only to that module's own limited kind of information. Fodor also suggested that cognitive modules are primarily perceptual, as in the example of the Muller-Lyer illusion, whereas central processing, that is, reasoning and decision making, is not. In addition, he suggested (but did not necessarily require, Coltheart 1999) that modules are fast, hardwired (i.e., neurally specific), and innately specified.

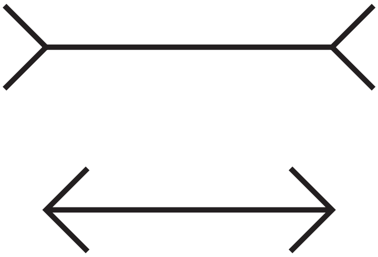

Figure B2.3. The Muller-Lyer illusion.

Many of the debates about cognitive modularity (e.g., Bolhuis and Macphail 2001; Flombaum, Santos, and Hauser 2002; Cheng and Newcombe 2005) seem to arise from a fixation on whether particular candidate cognitive modules meet all of Fodor's strict criteria (which are not always easy to decipher) rather than on the question, to what extent and in what ways, if any, is cognition modular? If instead we take domain-specificity of cognitive processing as definitional, the extent to which any candidate modular cognitive mechanism is central, is entirely encapsulated, depends on experience for its development, relies on a localized area in the brain, and so forth, becomes an empirical question (Coltheart 1999; Barrett and Kurzban 2006). Functionally modular cognitive mechanisms need not be associated with localized brain processes or be comparatively independent of experience for their development (for an extended discussion see Barrett and Kurzban 2006; Bateson and Mameli 2007). As we will see, extracting and storing information from the flow of events does not follow the same rules for all types of events, and thus learning mechanisms, (or memory systems, Sherry and Schacter 1987) are to some extent domain specific, that is, modular (Gallistel 1998; Shettleworth 2000; Gallistel 2003). Particularly good examples come from learning about space, time, and number (Chapters 8–10).

This is not to say that the concept of modularity is unproblematical. For example, if we identify a module as a domain-specific kind of information processing, how do we distinguish domains or a "kinds of information processing"? Evolutionary psychologists have promoted the metaphor of the mind as a Swiss Army knife, that is, a general-purpose tool made up entirely of special-purpose devices. But is there a module for everything? If a cheater-detection module (Chapter 12), or a face-processing module (Kanwisher 2006), why not hundreds of other modules beside (Fodor 2001; Buller 2005)? In learning theory the modularity debate takes the form of a debate about adaptive specializations *versus* general processes of learning (Section 2.5.2), but forthcoming chapters provide illustrations of how association formation is not the only way of acquiring information. At the same time, however, many candidate modular learning and memory systems share some fairly general properties such as sensitivity to duration and frequency of events. Thus modularity should not be emphasized at the expense of common features or connectedness. If nothing else, candidate modules are connected by virtue of being contained within the same individual. Modules may share sensory input systems, and, no matter how specific the triggering information, decision making, and behavioral output of a modular cognitive subsystem, central decision making of some sort is needed to set the animal's prorities for action. West-Eberhard (2003) recommends keeping the focus on connectedness and modularity at the same time by eschewing the term *module* and referring instead to developmental systems as more or less modular (see also Callebaut and Rasskin-Gutman 2005). Perhaps this recommendation can be applied to cognitive modularity as well.

illustrations. For instance, the superior colliculus, a visual processing area, is nine times larger in a 13-lined ground squirrel (a diurnal species) than in a laboratory rat (nocturnal), and in the blind mole rat, which spends its life underground, it is 38 times smaller than in a hamster. In the very dextrous raccoon, the sensory and motor areas devoted to the paws are greatly enlarged compared to those in other nonprimates (see Streidter 2005). Although these examples are exceptional in quantitative terms, because sensory systems are clearly evolved to allow each species to discriminate the stimuli most important to it (Chapter 3) it is not surprising to find sensory specializations reflected in species-specific tweakings of sensory organs and associated brain areas. However, suggestions that an analogous principle applies to cognition and the brain—in particular to an association between demand for spatial memory in the wild and size of the hippocampus—have been surprisingly controversial (Bolhuis and Macphail 2001; Macphail and Bolhuis 2001; Bolhuis 2005). Cognition is surely not exempt from evolutionary processes, so why should this be?

Figure 2.3 shows that among North American families of birds the three families with food-storing species all have, on average, larger hippocampi than expected for the size of the rest of their brains. The relationship between food storing and performance in tests of spatial memory is discussed in Chapter 7; here we delve into the relationship between food storing and hippocampus suggested by Figure 2.3. One can ask a number of questions about it. For example, what exactly does a bigger relative hippocampus consist of in neuroanatomical terms? How does a comparatively large hippocampus impact on the rest of the brain? How does it improve ability to retrieve stored food? For instance does a relatively large hippocampus increase the capacity or the durability of memory? These questions are still largely unanswered (see Bolhuis 2005), but some progress has been made in more detailed application of the comparative method to test the basic relationship shown in the figure.

Figure 2.3 classifies birds simply as food-storing or not, but in fact dependence on stored food varies considerably within both parids and corvids. For example, the Clark's nutcracker (Box 1.4) stores one type of food, pinyon pine seeds, very intensely during late summer and depends on its stores throughout the winter. The jackdaw, another corvid, does not store at all, and some other corvids store only moderately. Similarly, the great tit and blue tit do not store, whereas the willow tit and black capped chickadee store a great deal. These variations suggest looking within families at hippocampal volume as a function of dependence on storing. This has been done a number of times for both corvids and parids, with results coming out first one way (e.g., Hampton et al. 1995; Basil et al. 1996) and then another (Brodin and Lundborg 2003) as successive analyses have been more and more refined. It turns out that, for unexplained reasons, North American corvids and parids tend to have smaller hippocampi than European species, but when this continent effect is controlled for in cross-species comparisons, relative hippocampus size does correlate with food hoarding status in both corvids and parids (Lucas et al. 2004; Healy, de Kort, and Clayton 2005). Birds that store a lot also tend to have bigger brains overall than expected for their body size, perhaps reflecting sensory or motor specializations in behaviors for storing and retrieving food (Garamszegi and Eens 2004).

These analyses have all assumed that each species fits into a single category of hoarding intensity. However, some food storers such as black-capped chickadees have a very wide distribution, from rather moderate climates to areas with severe winters. One might expect differences between populations in such species. Accordingly, when chickadees from Alaska are compared to those from the lowlands of Colorado in tests in the laboratory, the Alaska birds store more, show better spatial but not color memory, and have larger hippocampi relative to brain size (Pravosudov and Clayton 2002). Since the birds in this study were taken from the wild, it is not known whether this hippocampal difference is present early in development or results from differences in food hoarding or other experiences in the wild. There are also many unanswered questions about details of hoarding-related changes in the brains of the chickadees in this and related studies (Bolhuis 2005; Sherry 2006).

Research on food-storing birds is but one set of tests of the more general hypothesis that spatial memory and hippocampus size should be related to demands on spatial memory in the wild (Sherry, Jacobs, and Gaulin 1992). Much of the work relating spatial learning and memory to territory size and migration discussed in Section 2.3.2 includes studies of the hippocampus (see Sherry 2006). An example involving sex differences comes from cowbirds. The females of several species of cowbirds lay their eggs in other birds' nests (i.e., they are nest parasites). The females of the brown-headed cowbird (*Molothrus ater*), a North American species, spend a good deal of their time in the breeding season prospecting for nests where potential hosts are about to lay. They need to remember the locations of many nests so as to be able to deposit an egg quickly when the host parent is absent at just the right time in its breeding cycle. Male brown headed cowbirds share none of this work, so they might be expected to have smaller hippocampi than females. And indeed the predicted sex difference is found for hippocampus relative to the rest of the brain in cowbirds, whereas there is no sex difference in two closely related species that are not nest parasites (Sherry et al. 1993). Making this story even more interesting, three other species of cowbirds are found in Argentina, only one of which behaves like the brown headed cowbird. In another, male and female prospect for nests together, and the third is not a nest parasite. Hippocampi of these three species show the pattern of species and sex differences in relative size predicted from the notion that participating in finding host nests requires exceptional memory (Reboreda, Clayton, and Kacelnik 1996). However, unlike the examples involving food storing or territory size, there is as yet little information on spatial memory in any of these birds in standardized laboratory tests (see Sherry 2006).

2.5 What does all this have to do with comparative psychology?

2.5.1 Function and mechanism and the comparative method

The kind of research summarized in the last section was dubbed *neuroecology* by Bolhuis and Macphail (2001). It has been criticized by these authors (see also Macphail and Bolhuis 2001; Bolhuis 2005) for supposedly confusing answers to Tinbergen's question about mechanism (e.g., how does cognition or the hippocampus work?) with answers to the question about function (e.g., what is spatial memory or the hippocampus good for?). This theoretical critique has tended to be combined with a defense of the overwhelming role of general processes in learning and memory and/or with claims that hippocampus, food-storing, and spatial memory are at best only weakly related.

Clearly, correlating features of the brain with food storing or any other ecologically relevant behavior does not show us directly *how* the brain works but rather what it allows the animal to do. Nevertheless, knowing what something does can provide valuable clues as to how it works. Figure 2.12 is an example borrowed from Richerson and Boyd (2005). To quote Sherry (2005, 449), "Causal explanations must meet design criteria that are set by the function of behavior." Therefore, the study of adaptation (or current function), with which we began this chapter, has a role in the study of cognition and the brain. A critical application of the comparative method–a solid data set with many cases of independent evolution and checks that other areas of the brain are not also correlated with the same behavior or ecological factor—provides strong evidence that particular behavioral and neural characters evolved together. Additional data could perhaps give us a picture of the sequence of events in evolution. For example, de Kort and Clayton (2006) suggest that a phylogeny of corvids shows ancestral corvids were moderate cachers, and therefore that food caching has become more intense in some species while being lost in others. And of course the correlational evidence characteristic of the comparative method is rarely interpreted in isolation. For example, behavioral and lesion studies of individual species clearly show that the hippocampus is involved in spatial memory and cache retrieval. In the example in Box 2.2, we know very little about what innovativeness or behavioral flexibility means in terms of specific cognitive and brain mechanisms, so this is a case in which findings from the comparative method may suggest new kinds of naturalistic tasks that could be used to compare species behaviorally.

The idea that cognitive science can advance by analyzing the information processing tasks that organisms are designed to do has been profitably applied to the study of perception (Marr 1982; Shepard 1994). Among the most prolific and eloquent proponents of the view that thinking about the evolved function of cognition is the best way to understand how it works are the evolutionary psychologists Leda Cosmides and John Tooby (e.g., Cosmides and Tooby 1995; Tooby and Cosmides 1995). One prediction of this adaptationist point of view is that distinguishable cognitive mechanisms or modules (Box 2.3) will evolve whenever the information-processing problems a species has to solve require different, functionally incompatible, kinds of computations (Sherry and Schacter 1987). These modules will be

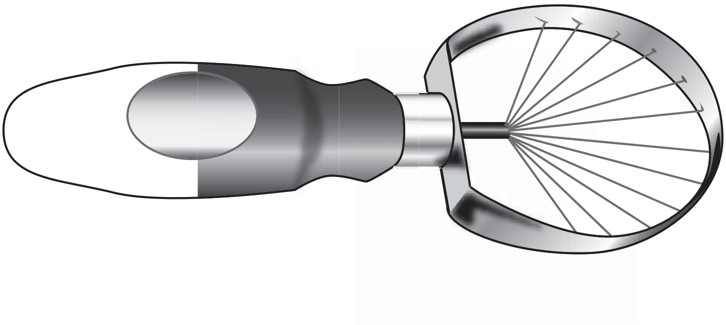

Figure 2.12. What is this? For the answer, see Figure 2.14 at the end of the chapter.

domain-specific, that is, each one will operate only on a restricted appropriate set of inputs, for example information about physical causation, time, space, or social relationships (see Gallistel 1998; Shettleworth 2000).

A second key prediction of the adaptationist viewpoint is no organism is the proverbial tabula rasa, or blank slate. Rather, animals' nervous systems are preorganized to process information in species-appropriate ways. Not only such specialized learning abilities as bird song (Chapter 1) but also associative learning, memory storage, attention, and problem solving as well as perception are matched to specific environmental requirements. Thus, cognitive scientists should be seeking to understand the structure of information-processing in terms of the structure of the world. For example, Cosmides (1989) claims that the ability to solve the Wason selection task, a logical problem, reflects an ability that was selected because it helped in detecting cheaters on social contracts. This notion predicts that people should reach the logically correct solution more often with problems about detecting cheaters than with formally identical problems about other material. Although many data are consistent with this hypothesis, it has not gone unchallenged (Chapter 12). The same kind of argument has been applied to experimental tests of the adaptive value of Pavlovian conditioned responding (Chapter 4). Such research is implicitly based on the argument from design: "X appears to be designed specifically to do Y; if it is, then animals with X should be better at Y than at some superficially similar but adaptively irrelevant task, Z."

The evolutionary psychologists' approach is essentially the same as the approach to cognition taken in this book. However, it faces several problems. Some stem from the indirectness of the relationship between cognition and fitness depicted in Figure 2.7. As Lehrman put it, "Nature selects for outcomes, not processes of development" (Lehrman 1970; Shettleworth 1983; Rozin and Schull 1988). Function does not uniquely determine the details of causation (Hogan 1994a; Bolhuis 2005). For instance, if the adaptive problem solved by eggshell removal is reducing predation, why didn't gulls evolve eggshells that were cryptically colored inside? The answer to this sort of question may lie in constraints from other aspects of the species' biology. The way in which eggshells are produced in the gull's oviduct may not readily allow for a change in the color of their interior, whereas gulls need motor patterns for picking things up and carrying them in foraging and nestbuilding, and these could be used equally well to carry eggshells. To take an example from cognition, many animals need to be able to return to a home to care for their young or to gain protection from predators. Thus they need a cognitive device for remembering and relocating places, but its details may differ from species to species. For example, dead reckoning (path integration) is accomplished very differently by rats and ants (Chapter 8). Similarly, because animals are selected to care for their own offspring rather than unrelated young, species with parental care must have mechanisms for recognizing their own offspring, in some sense. This can mean nothing more sophisticated than spending a couple of weeks stuffing food into any gaping mouth in your nest, but animals with young that run around while their parents are still feeding them need another mechanism, such as mutual learning of identifying cues. Thus although the prediction that offspring should be favored does not tell us how a particular species recognizes its young, a closer look at the species' biology may make functional sense of the mechanisms by which it does so. Conversely, identifying the function of a process discovered in the laboratory can raise new mechanistic questions that would not have been asked otherwise (Sherry 2005).

2.5.2 Adaptive specializations and general processes

If an ability is an adaptation to certain ecological requirements, it should vary quantitatively across species with those requirements. More spatial information to process means more capacious spatial memory (section 2.3.2); reliance on olfaction for foraging at night means relatively bigger olfactory bulbs (in birds anyway, see Healy and Guilford 1990); more complex social groups may mean better-developed social cognition (Chapter 12). These statements describe adaptive specializations of characters that species share. Such variations are readily observed in characters like beaks in birds (Figure 2.13). A bird that drinks nectar needs a long narrow beak, one that lives on hard seeds needs a beak like a nutcracker, one that tears flesh needs a hooked beak. Of course such changes are rarely confined to a single character but must be accompanied by adaptations of the digestive system, prey-catching behavior, habitat preference, and so on. As Darwin argued, evolutionary change can be seen as resulting from gradual modifications from some ancestral state. As a result, the characters of any given species are both unique, or adaptive specializations, and general, or shared with many other species.

Unfortunately, in the study of learning adaptive specialization has too often been set in opposition to general processes (Macphail and Bolhuis 2001). There is a historical reason for this. *Adaptive specialization* was introduced into discussions of learning by Rozin and Kalat (1971) in a landmark paper about flavor aversion learning and other newly described phenomena that seemed to reveal qualitatively new kinds of learning. For example, rats learned aversions to flavors that were followed by illness even when a single experience of illness had followed sampling of the flavor by many hours. Flavor aversion learning seemed to be comprehensible only by thinking of animals in the laboratory *qua* animals rather than *qua* model humans or general learning machines. In fact, conditioned flavor aversion and related findings turned out to have the same properties as other examples of associative learning, but with quantitatively special—and functionally suitable—parameters (Chapter 4). Thus they illustrate in a very compelling way how general processes of learning are expressed in a species- and situation-specific way, that is, with quantitative specializations. Just as with the debates about concerted vs. mosaic evolution of the brain, or general intelligence vs. modularity, the truth about general processes vs. adaptive specializations is "both."

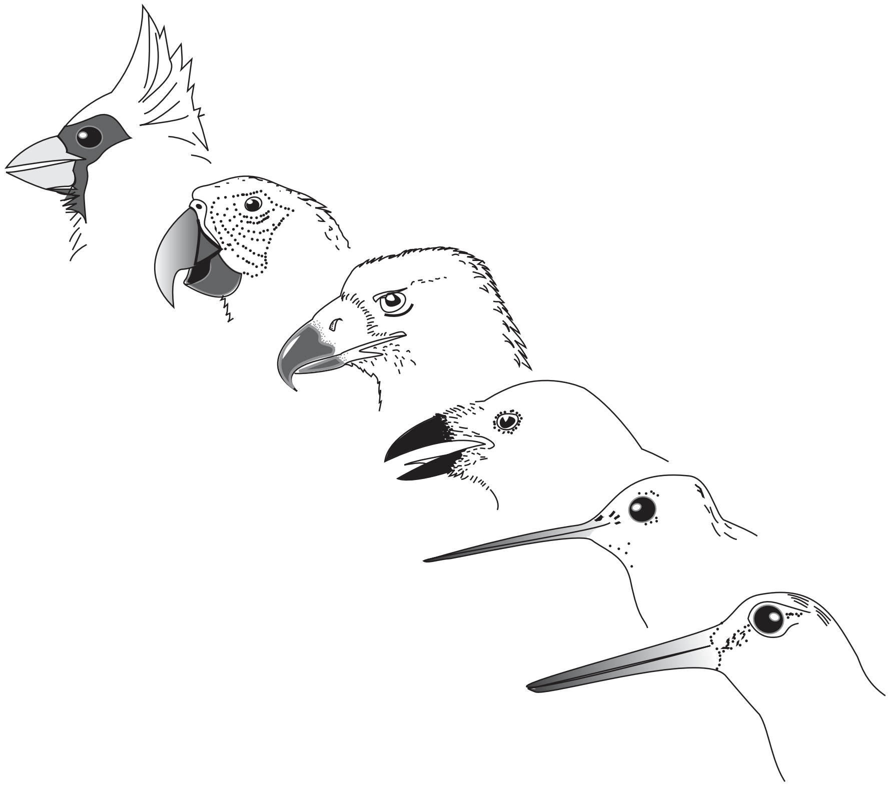

Figure 2.13. Some adaptations of birds' bills for different modes of feeding. From left to right, a seed cracker, nut cracker, meat tearer, generalized forager, flower prober, and earth prober. After Welty (1963) with permission.

In any case, opposing generality and specialization is biologically incorrect. Commonality and diversity are two sides of the same coin (Rozin and Schull 1988), and one should not be emphasized at the expense of the other. People interested in general processes have tended to compare species widely separated on the evolutionary tree, for example pigeons and rats as in Box 1.3, whereas the study of adaptive specializations is associated with comparison of close relatives chosen for having different behaviors in the wild. As Papini (2002) has argued, both approaches have much to reveal about the phylogenetic distribution and evolution of learning mechanisms, just as they are doing with genetics and neurobiology.

Thinking in terms of function and evolution, of convergences and divergences of both close and distant relatives, is a tremendously powerful tool in comparative psychology. For example, we learn in Chapter 10 that monkeys but not pigeons solve a test of transitive inference in a way that suggests they form a representation of an ordered set of items. That is, when exposed to training designed to teach them, in effect, "green is better than red," "red is better than blue," "blue is better than yellow," "yellow is better than purple," monkeys behave appropriately (i.e., choose red) when presented with the novel red and yellow pair and pass further tests that pigeons fail. Is this simply a mammal-bird difference, a difference in general intelligence perhaps? But asking what transitive inference might be good for in the real world suggests that it is useful for animals that form social hierarchies, regardless of whether they are mammals or birds. And here the general study of animal behavior becomes integrated with investigations of the generality of this cognitive process in suggesting species to study. The corvids include species with and without dominance hierarchies, thus providing subjects for one test of whether the ability to “do” transitive inference is confined to primates or is convergently evolved in species living in groups that need a certain kind of social intelligence (Kamil 2004; Paz-y-Mino C. et al. 2004). Thus integrating investigations of mechanistic and functional questions about cognition does not mean confusing the answers to different sorts of questions but rather developing a science in which information about how cognition may be used informs investigations of how it works.

2.6 Summarizing and looking ahead

Just as Chapter 1 introduces the study of comparative cognition, this chapter introduces the study of evolution and adaptation. A claim that any character is adaptive can be tested in three ways: by modeling, to discover how well the character serves a hypothesized function; with the comparative method, to test whether variations in the character across many species are related to variations in ecology; and by experiment. Ideally two or more of these methods can be used together. Using the comparative method requires good inferences about the phylogeny of the species being compared. Evolutionary psychologists claim that

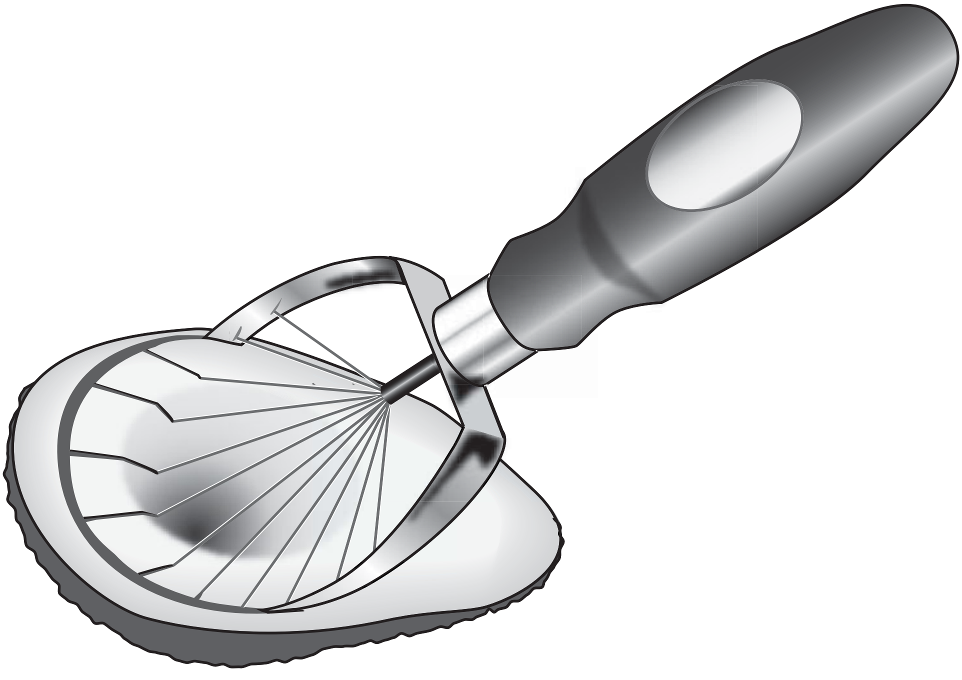

Figure 2.14. The object in Figure 12.12 is an avocado slicer.The sharp curved edge separates the pulp from the outside of the avocado and the thin wires make neat, equal-sized, slices. Richerson and Boyd (2005) used this example of how knowing what something designed to do helps to understand its structure.

understanding how cognitive mechanisms evolved and what they are for can help us to understand how they work. However, testing evolutionary hypotheses about cognition can be difficult because cognitive processes affect fitness indirectly, through the medium of behavior.

We have encountered three sets of contrasts in this chapter that seem intuitively to have much in common: Mosaic vs. concerted evolution, modularity vs. connectedness, adaptive specialization vs. general process. All seem to express a tension between a focus on parts with their specific properties and a focus on a whole with what its parts have in common. In the long (or maybe not so long) run, the kinds of processes they refer to may be linked mechanistically; developmental modularity is already being linked with evolution (West-Eberhard 2003; Schlosser and Wagner 2004). In any case, the conclusion to be drawn from discussion of each of these contrasts is that the truth is usually a mixture of both. It may be human nature to focus on only particularities or only wholes, but "It would be difficult to overemphasize the importance of agility in being able to appreciate both the modularity and the connectedness of biological organization" (West-Eberhard 2003, 83).

Further readings

Most of the topics in this chapter are covered in greater depth for students in Papini's (2008) *Comparative Psychology* and the behavioral ecology text by Danchin, Giraldeau, and Cezilly (2008). For understanding the theory of evolution there is no substitute for reading at least part of *The Origin of Species* (Darwin 1859) or *The Descent of Man and Selection in Relation to Sex* (Darwin 1871). Stearns and Hoekstra (2005) is a current introductory text. Evolutionary theory and its application to behavior have been the subject of some outstanding books for the general reader. Richard Dawkins's (1976) *The Selfish Gene* is already a classic exposition of the basics of behavioral ecology. *Darwin's Dangerous Idea* (Dennett 1995)is a philosopher's discussion of evolutionary theory and its wider implications. *The Beak of the Finch* (Weiner 1994) is a very readable account of studies of evolution in action on the Galapagos, now updated by Rosemary Grant and Peter Grant's (2008) own account of their work and its implications.

For brain evolution, Streidter's (2005) clear and fascinating text is highly recommended, as is Healy and Rowe's (2007) thoughtful review of comparative studies of the relationship between brain size and complex cognition. Two thoughtful reviews by Sherry (2005, 2006) analyze the debate surrounding neuroecology and review recent developments. For an extended discussion of the debate about modularity along the same lines as Box 2.3, the review by Barrett and Kurzban (2006) is recommended. It also incorporates considerations from human evolutionary psychology.

Part I

Fundamental Mechanisms

Cognitive mechanisms are generally defined functionally, that is, by what they do, but the specificity of these functions varies tremendously. For instance, principles of perception, memory, or discrimination learning are pretty much the same regardless of the kind of information being perceived, remembered, or discriminated, whereas by definition principles of numerical, spatial, or social cognition apply only in particular cognitive domains. But the mechanisms involved in assessing numerosity, traveling in space, interacting with others, and so on cannot be understood in isolation from domain-general principles of perception, learning, and memory. Although cognition may be modular to some extent (Box 2.3), it is impossible to appreciate what may be unique to individual cognitive domains without first appreciating some fundamental principles that cut across some or all of them.

Accordingly, Chapters 3–7 lay the groundwork for the parts of the book dealing with specifically physical and social cognition. Chapter 3 describes fundamental mechanisms of perception in the context of their evolution and ecology. Chapters 4–6 introduce basic mechanisms of learning: how animals associate events, recognize single objects, and learn to discriminate among things and classify them. Chapter 7 looks at basic principles of memory, concluding with controversial attempts to discover whether other animals have conscious memories as humans do. Some of the issues discussed in these five chapters are among the oldest and most-studied in comparative psychology, but as we will see they continue to inspire new discoveries and lively debates.

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3
Perception and Attention

To a bat or an owl, a summer evening is full of sounds of which we are only dimly aware. A honeybee sees patterns on flowers that are invisible to us. That every kind of animal has its own *umwelt* or self-world, formed by the kinds of information its senses can process, was one of the fundamental insights of the founders of ethology. The ethologist Von Uexküll (1934/1957) attempted to capture this insight in pictures of how the world might seem to other species (Figure 3.1). A great deal is now known about how animals process sensory information even if most contemporary behavioral scientists do not attempt to translate it into such depictions of subjective experience.

The study of comparative cognition begins with sensation and perception for two reasons. First, it is important to keep in mind that adaptive behavior can result from specializations in perception as much as from higher-level learning or decision processes. Second, perception provides some excellent examples of modularity and adaptation in information processing. This chapter begins with a few illustrative examples of sensory specialization, then looks at how perception can be studied in animals and introduces the important ideas of signal detection theory. Armed with this information, we can see how "receiver psychology" (Guilford and Dawkins 1991; Endler and Basolo 1998; Rowe and Skelhorn 2004) has influenced the evolution of animal signals. And at the end of the chapter we look at how sensory information is filtered by attention and how attentional processes can explain the classical ethological phenomenon of search image formation.

3.1 Specialized sensory systems

Every animal must be able to respond appropriately to its own food, mates, young, and predators. The cues it can use are determined by the environment characteristic of its species (Dusenbery 1992). Species active at night have a different set of cues available to them from those active during the day; those that live underground, different cues from those that live in the treetops; creatures of the deep sea, different cues again from creatures of clear streams. Sensory systems and their sensitivities tend to be matched to lifestyle and environment.

The sensory specializations we find most impressive are those allowing animals to respond to forms of energy that an unaided human cannot detect. The ultrasonic

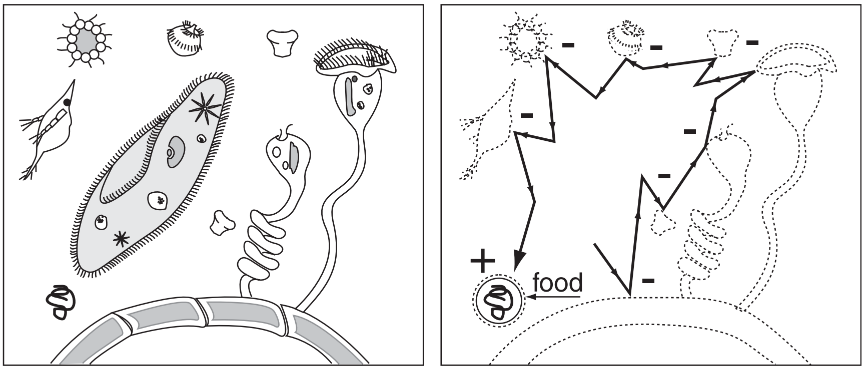


Figure 3.1. Von Uexküll's conception of the *umwelt* of a paramecium (the large gray blob in the left panel). The environment in all the complexity perceived by humans is depicted on the left, the same environment as perceived by the paramecium on the right, with + and—_ showing what attracts and repels it, respectively. Redrawn from von Uexküll (1934/1957) with permission.

hearing of bats is one well-studied example (Figure 3.5). Many bat species find prey in the dark using a kind of sonar. They continually emit ultrasonic cries, and the echoes from flying insects enable the bats to locate their prey in complete darkness. Some snakes locate live prey by homing in on warm objects, using infrared detectors in their snout. The platypus feeds underwater at night using sensitive receptors in its bill to detect the electric fields generated by movements of its prey (Manger and Pettigrew 1995). Using mechanisms that are still somewhat mysterious, some birds, mammals, reptiles, and other animals navigate by means of the intensity and/or inclination of the Earth's magnetic field (Wiltschko and Wiltschko 2006).

Many animals with color vision, such as honeybees and most birds, have a different pattern of wavelength sensitivity from humans. Thus they do not necessarily see prey items or potential mates (or images we create to mimic them) the way we do (Box 3.1). For example, wavelength sensitivity of many birds extends into the ultraviolet (UV), and some feathers reflect UV light (Cuthill et al. 2000). This discovery has led to some striking observations which illustrate very compellingly how we need to understand an animal's species-specific perceptual world to understand its behavior. For example, blue tits and starlings are bird species in which males and females look the same color to humans. But to a blue tit or starling, males look very different from females because they have conspicuous patches of UV-reflecting feathers, patches which are larger or better developed in males. In such species, females may base mate choice on the brightness of these patches, rejecting males treated with UV-blocking sunscreen in favor of untreated males (review in Cuthill et al. 2000). To take an example from prey-catching, kestrels locate places where voles can be found using the UV reflectance of the urine that the voles deposit as they run along their habitual trails (Viitala et al. 1995). Honeybees also have UV vision, which they use to discriminate among flowers (Section 3.5.1).

The foregoing are but a few examples of striking species differences in what animals sense. The sensitivity of particular systems also may differ among closely related species or even individuals of the same species. For example, optimal visual sensitivity is different for fish dwelling at different depths because the distribution of wavelengths illuminating objects changes with depth as sunlight is filtered by seawater. Sensitivity may change with age if the same fish lives at different depths at

Box 3.1 Color Vision

Color resides not in objects but in the observer's perception of wavelength differences and similarities. To a color blind animal, objects differ visually only in brightnesss. What this means is illustrated by a classic demonstration of color vision in honeybees (Frisch 1914, as cited in Kelber, Vorobyev, and Osorio 2003). Bees trained to find sugar water on a blue or a yellow card showed that they were using wavelength and not brightness by choosing their training color over all shades of grey, from very light to very dark. The first stage in responding to wavelength is the reaction of photopigments to light; in vertebrates these are in the retinal cone cells (cones). Each photopigment has a unique profile of responsiveness as a function of wavelength. Behavioral discriminations are based on a neural comparison of the responses of different photoreceptor types (for further details see Cuthill et al. 2000; Kelber, Vorobyev, and Osorio 2003).

The kind of color vision available to different species is revealed by the relative sensitivities, or absorption spectra, of the animals' photoreceptor types (Figure B3.1). Honeybees, like many other insects (Briscoe and Chittka 2001), have three photoreceptor types all near the blue-green end of the spectrum. One is sensitive in the ultraviolet. Pigeons have three photoreceptor types (retinal cone cells, or *cones*) with sensitivities similar to those of humans' and a fourth with maximum sensitivity in the ultraviolet (UV). Many other birds have UV vision, as discussed in the main text. Humans and many other primates have three cone types, with maximum sensitivities in red, green, and blue wavelengths. Primates are unique among mammals in having color vision, and there is some debate about why such trichromatic color vision evolved (Surridge, Osorio, and Mundy 2003). Red-green discrimination is thought to be useful for detecting ripe fruits in the forest, but it could be equally useful for folivorous (leaf-eating) primates because the freshest and most nutritious leaves tend to be red. Color also plays a role in social communication in some primates (Ghazanfar and Santos 2004), but whether it evolved first in that context or in the context of foraging is still debated. Selection for enhanced visual capabilities, including color vision, may have played a role in the evolution of relatively large brains in primates (Chapter 12; Barton 2000).

Behavioral tests of color matching are important in showing how photoreceptors are actually used: any wavelength can be matched with a mixture of the primary colors for that species (i.e., those at the peak sensitivities for the different photoreceptors). This principle is made use of in video screens that generate colors by activating red, green, and blue phosphors in different proportions for different colors. As a result, most animals do not see the colors on conventional TV the way we do because their peak sensitivities and/or distributions of different receptor types are different from ours (Box 6.1; Oliveira et al. 2000).

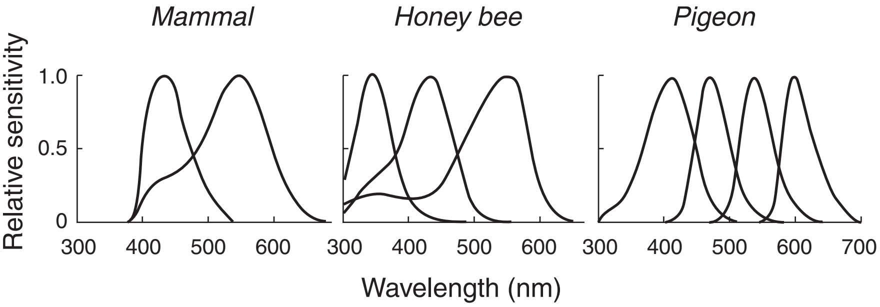


Figure B3.1. Relative wavelength sensitivities of photoreceptors in a representative nonprimate mammal, honeybees, and pigeons. In terms of human perception, red is toward the right on the x-axis. Relative sensitivity, on the y-axis, is the proportion of maximum responsiveness that the given receptor type shows at each wavelength. Human sensitivity is similar to that of pigeons except that we lack the very short-wavelength, UV, receptor. Adapted from Kelber, Vorobyev, and Osorio (2003) with permission.

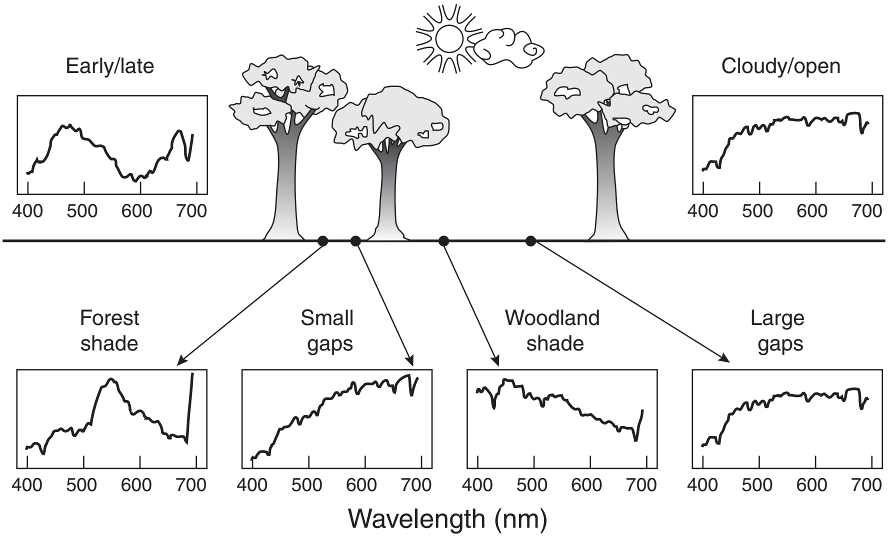


Figure 3.2. The relative intensities of different wavelengths of light in different parts of a forest and under different conditions. Forest shade, for instance, has a relatively high proportion of wavelengths from the middle (greenish) part of the spectrum, whereas small gaps are rich in longer (redder) wavelengths. Redrawn from Endler (1992) with permission.

different stages of its life cycle (Lythgoe 1979). As shown in Figure 3.2, the light environment also differs in different parts of the forest and at different times of day. The nuptial plumage of male forest birds and the times and places at which they display may be matched to the available light in such a way as to maximize the males' conspicuousness (Endler and Thery 1996; Endleret al. 2005). The sound frequencies that travel farthest are determined by factors such as atmospheric conditions and type of vegetation. These physical constraints have affected the evolution of animal sound production and reception mechanisms. For example, the songs of forest birds tend to have a different distribution of frequencies from the songs of birds from open habitats. Regardless of habitat, many birds choose to sing from high, exposed, perches, from which sound travels furthest (Catchpole and Slater 1995; Slabbekoorn 2004).

How much of the environment an animal can see at once depends on where its eyes are. Animals with eyes on the sides of their heads can see a wider arc of their surroundings than animals with frontally placed eyes. The placing of the eyes reflects the extent of binocular vision required by the species diet and the extent to which the animal is predator as opposed to prey, as illustrated in Figure 3.3 with the striking contrast between an owl and a woodcock. The most important things may be near the horizon or above or in front of the animal, and this feature of ecology may be matched by greater visual acuity in some parts of the visual field than others. For example, pigeons view a small area in front of them binocularly. Binocular vision and concomitantly good depth perception are important for accurate pecking at seeds, whereas the lateral field of view is important for detecting predators. Accordingly, pigeons have two "foveas," areas of maximally dense photoreceptors, one in the binocular field and one on which objects to the side are focused (see Roberts et al. 1996). Species of birds with different lifestyles also have different retinal distributions of photoreceptors (Nalbach, Wolf-Oberhollenzer, and Remy 1993). For example,

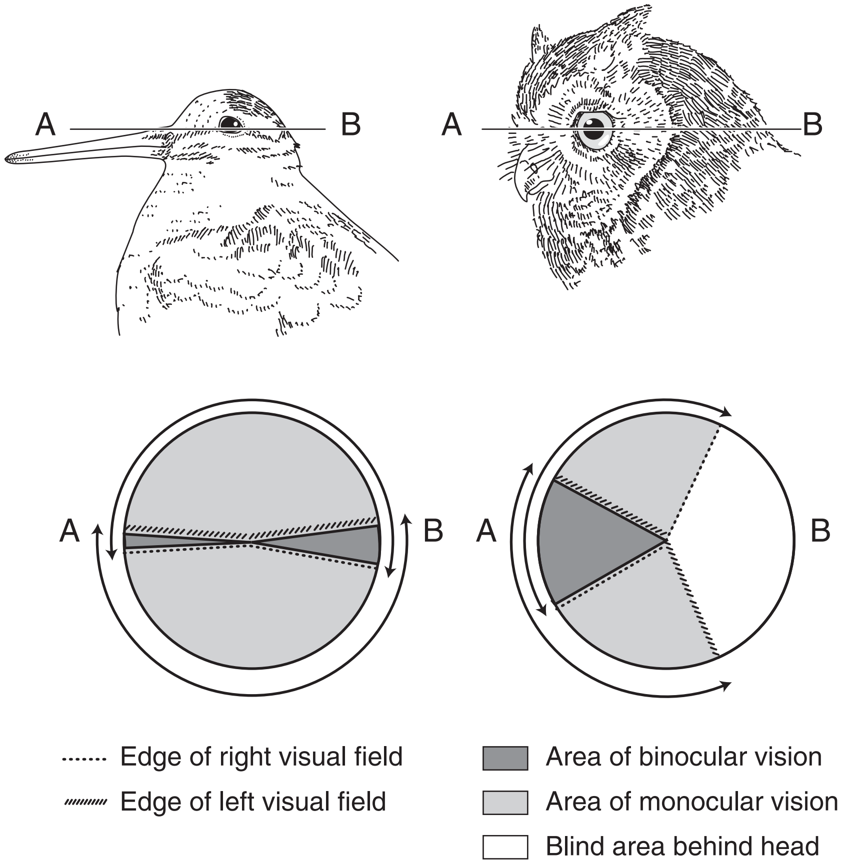


Figure 3.3. Differences in the placement of the eyes and visual fields for different lifestyles, prey animal (wood cock) versus visual predator (owl). Redrawn from Evans and Heiser (2004) with permission.

seabirds tend to have a central horizontal strip of high density photoreceptors. Owls and other birds of prey have the densest photoreceptors in the part of the retina that views the ground. They may have to turn their heads almost upside down to see something approaching from above.

In many situations animals respond to a very narrow range of stimuli. For example, male moths of species like *Bembyx mori* are sexually attracted to a particular molecule contained in a pheromone emitted by the female of their own species (see Hopkins 1983). A hungry baby herring gull pecks at a red spot near the end of its parent's beak and less at other colors in other locations (Tinbergen and Perdeck 1950). The first step in analyzing such an example of selective behavior is to find out whether it can be explained by the responsiveness of the sensory system involved. In the case of the moth, the characteristics of the olfactory system completely account for the male's selective sensitivity. The male moth's antennae are covered with receptors selective for the female's sexual pheromone. In contrast, the herring gull's selective pecking at red spots on beaklike objects reflects processing at a higher level (Delius et al. 1972). Both the female pheromone and the red spot would be classified as sign stimuli (Chapter 6), but one reflects a purely sensory filter, the other a more central processing mechanism.

3.2 How can we find out what animals perceive?

3.2.1 Studying perception in animals

Three approaches can be taken to analyzing perception in animals: *(1)* electrophysiology and related methods of neuroscience, *(2)* studying how natural behavior changes with changes in stimulation, and *(3)* testing learned behavior with the methods of animal psychophysics. Each one of these approaches has its advantages and disadvantages. Two or three of them can be used together to understand selective responsiveness in natural situations.

Recording electrical responses of sensory neurons to controlled stimuli (electrophysiology) is the most direct way to find out what sensory information is potentially available to an animal. In the case of the moths described in the just-preceding section, such methods make clear that the "decision" to approach and court another moth is reached by the olfactory receptors. However, to find out what features of the world are behaviorally significant, it is necessary to go beyond electrophysiology and look directly at behavior. Often, an animal's natural behavior to stimuli of importance to it can be used to test simple sensory discriminations. For example, hamsters, like many other mammals, mark their territories with secretions from special glands. To find out whether they can discriminate among the scent marks of different individuals, Johnston et al. (1993) made use of the fact that a hamster spends a great deal of time sniffing a glass plate scent marked by another hamster. This response decreases as the hamster encounters successive marks of the same kind from the same hamster, that is, the response *habituates* (see Chapter 5). However, once the subject hamster has habituated to the scent from one hamster, it still vigorously investigates scent from a second hamster (Figure 3.4). Such renewed investigation shows that the animal discriminates the second scent from the first. As we will see in later chapters, this is a powerful way to discover what stimuli all kinds of subjects, including humans, discriminate. It is generally called the *habituation/dishabituation method,* but it should be noted that renewal of an habituated response in the presence of a new stimulus is not strictly the same as what is referred to as dishabituation in the analyses of the habituation process discussed in Chapter 5.

The differences animals perceive among behaviorally relevant stimuli can be studied in the field as well as in the laboratory. For example, many territorial songbirds learn the characteristics of their neighbor's songs and where those neighbors typically sing (Box 5.1). A familiar neighbor singing from a new location is treated as

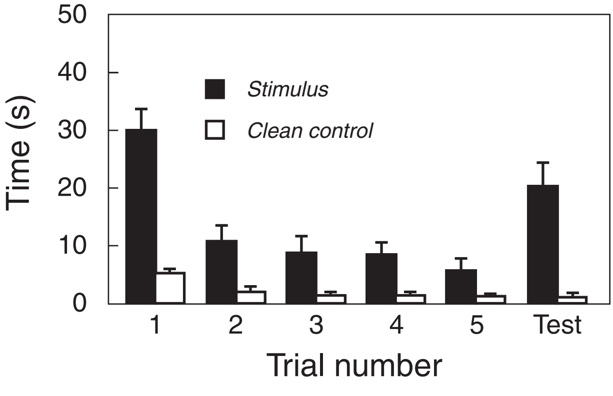


Figure 3.4. Data from a habituation/dishabituation test of olfactory discrimination in male golden hamsters. Time spent sniffing the scented (stimulus) half of a glass plate is compared to time spent sniffing the clean half. The stimulus was the same in Trials 1–5 and different in Trial 6. Redrawn from Johnston et al. (1993) with permission.

a threat and attacked. A novel conspecific song from a loudspeaker is also attacked (Falls 1982), making it possible to present songs in a controlled way in the field to find out what aspects of this complex auditory stimulus birds are sensitive to. Experiments of this kind have shown, for example, that great tits can discriminate among the voices of their neighbors (Weary 1996).

A limitation of using natural responses to natural stimuli is that there are at least two reasons why an animal may respond in the same way to two or more stimuli. It may not be able to discriminate among them or the differences it discriminates may have no behavioral significance for it. In the example above, for instance, a territorial male bird might be equally aggressive toward two very different novel songs, but he might later show that he could discriminate them if one was the song of a neighbor while the other remained relatively novel (for further discussion see Collins 2004; Dooling 2004). Late in the breeding season, when sex hormone levels are lower, he might respond equally little to all songs. A good understanding of the behavior of the species being tested is clearly necessary to ensure that tests of discrimination are being done in a meaningful way. In general, because natural responses to natural stimuli may reflect so many motivational and other variables, electrophysiological or psychophysical methods must be used to study sensory ability separately from responses to the signals of interest.

3.2.2 Animal psychophysics

One of the oldest areas of experimental psychology is *psychophysics,* the study of how information is processed by the senses. For example, what is the smallest amount of light energy, at each wavelength, that can be seen in total darkness? Or, with a given background sound, what increase in sound pressure level is required for subjects to report an increase in loudness? The former is a question about the *absolute threshold;* the latter, about the *relative* or *difference threshold.* Data from psychophysical investigations typically consist of plots of absolute or relative thresholds as a function of a physical stimulus dimension.

A psychophysicist interested in absolute auditory thresholds can tell a human subject, “Press this button whenever you hear a tone.” Visual acuity can be tested by instructing a person, “Press the left button when you see stripes; press the right when you see a gray patch.” Animals, in contrast, have to be given their instructions by careful training, using the methods of operant or classical conditioning. Figuring out how to ask nonverbal subjects the questions one wants to ask in a way that yields unambiguous answers is one of the biggest challenges in any area of comparative cognition. With operant methods, the animal is placed in a situation where it can obtain reward or avoid punishment only by using as a cue the stimulus the experimenter is interested in. Since animals seem to have an uncanny knack of latching onto subtle irrelevant cues, being sure the animal responds only to the stimulus of interest is not as easy as it sounds. Well-designed psychophysical experiments include stringent controls for possible influences of extraneous cues.

A typical procedure for investigating animal sensory abilities is one used for testing bats’ ability to discriminate distances by echolocating (Figure 3.5). The basic idea is to reward a bat for making one response when it detects an object moving rapidly back and forth (a “jittering” target) and another response when the target is stationary. As long as the bat can make the correct choice at above the chance level of 50%, it must be discriminating between the two distances from which it hears the jittering target’s echoes, that is, between the two echo delays. Since all bats are not really “as blind as a

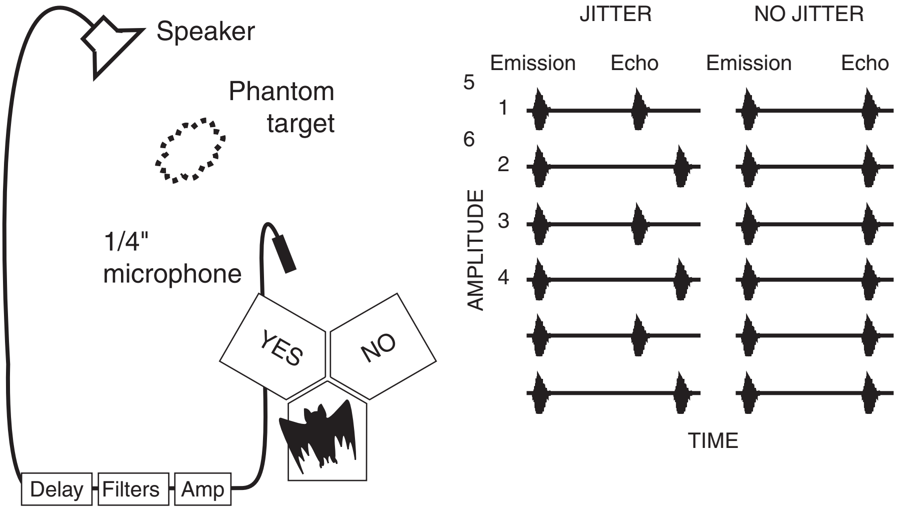


Figure 3.5. Schematic view of a setup for testing temporal discrimination in bats. The bat was reinforced for moving onto the left platform for a jittering target ("yes, jitter present") and onto the right platform when no jitter was present. Redrawn from Moss and Schnitzler (1989) with permission.

bat," the experiment depicted in Figure 3.5 had to eliminate visual cues to motion. This was done by using virtual rather than real targets. The bat's cries were picked up by a microphone near its mouth and broadcast back to it either with a fixed delay, as if reflected by a stationary object, or with alternating short and long delays, as if coming from a jittering object. The bat sat on a Y-shaped platform and was rewarded with a mealworm for crawling onto the left arm when a (virtual) jittering target was presented and onto the right arm for a stationary one. To ensure that the animal learned the required discrimination, training began with large jitters. When the animal performed correctly a large proportion of the time on this easy task, the task was made more difficult, and so on. The bats were eventually making extremely fine discriminations.

This elaborate instrumentation and training procedure may suggest that psychophysical experiments can be done only in the laboratory, but this is not so. Classic field studies of bees' color and shape perception were done by von Frisch (1967) and similar methods have been used with hummingbirds (Goldsmith, Collins, and Perlman 1981). Animals that return repeatedly to one food source as bees and hummingbirds do are particularly good candidates for field tests of sensory abilities because the animal is using the sense for the job it has most likely evolved to do. Not all training methods used in animal psychophysics are so obviously related to the subjects' natural behaviors. It might be assumed that any arbitrary training procedure may be used to tap the capabilities of any sensory system, but the results of psychophysical studies could be influenced by the motivational and response systems used. For example, pigeons attend more to lights than tones when working for food but the reverse is true when they are avoiding shocks (Foree and LoLordo 1973). This could mean that subtle auditory discriminations are easier to teach to frightened than to hungry pigeons. The kind of behavior guided by a given sensory system should be taken into account in psychophysical tests of that system.

3.3. Some psychophysical principles

All sensory systems have some basic properties in common (Barlow 1982), many of them shared by instruments designed to detect physical energies. As we have already seen, the senses are characterized by specificity in the kinds of energies they detect: the visual system is specific for electromagnetic radiation in a certain range of wavelengths; the auditory system for changes in sound pressure; the olfactory system for airborne chemicals. Moreover, most sensory systems are not equally sensitive to everything they detect. Rather, each system can be characterized electrophysiologically and behaviorally by a tuning curve. The plots of visual sensitivity as a function of wavelength in Box 3.1 are examples.

In addition to quality ("what is it?") an important feature of stimuli is intensity ("how much is it?"). Brightness, sweetness, and loudness are examples of perceptual intensity continua. An important psychophysical principle that emerges from research on perception of intensity or size continua is Weber's Law, which describes the difference threshold (or *just noticeable difference,* the *JND*) between two stimuli as a function of their magnitude. The JND is a constant proportion across a wide range of base values. This proportion, the Weber fraction, depends on the species and sensory channel. For example, suppose a 10-gram weight has to be increased by .5 grams in order for a person consistently to detect the change. Weber's Law says that if we ask for the same judgment starting with a 20-gram weight, the difference threshold will be 1 gram, whereas it would be .25 grams if we started with a 5-gram weight. Examples of Weber's Law in animals' time and number discrimination are discussed in Chapters 9 and 10.

Three other psychophysical principles have important implications for animal behavior. First, sensory neurons tend to respond more to physically more intense stimuli. Therefore, more intense or reliable behavioral responses can be expected to stimuli that are brighter, louder, or bigger in some other way. This seems so obvious and right as hardly to need stating, but animals need not have been designed this way. One could build, say, a sound meter that gave high readings to soft sounds, and none at all to loud ones. An animal built like it would react to things far away from it and ignore predators or conspecifics close by. In fact, the opposite is generally the case, and it does make functional sense that animals should react more intensely to things that are larger and/or closer.

A second general feature of sensory or perceptual systems is a tendency to habituate (or show adaptation) to prolonged unchanging stimulation. We have seen in the last section how this feature has been put to use to test hamsters' odor sensitivity. It has been suggested that the tendency for listeners to habituate explains why some bird species have repertoires of many different songs. Females, it is suggested, will be more stimulated by a constantly changing series of songs than by one song sung monotonously over and over, and indeed in some species males that sing more different songs are more successful in obtaining mates (Collins 2004).

Third, in many systems response to a given stimulus depends on its contrast with the background. A quiet tone is more easily heard in silence than in soft noise. To a person with normal color vision, a red spot looks redder on a green than on an orange background. The tendency of sensory systems to respond more strongly to stimuli that contrast with what surrounds them in time or space appears to have shaped the evolution of animal color patterns, auditory signals, and the like. For example, many animals that are food for other animals resemble the substrate on which they typically rest, that is, they minimize contrast so as to be cryptic rather than conspicuous. Such

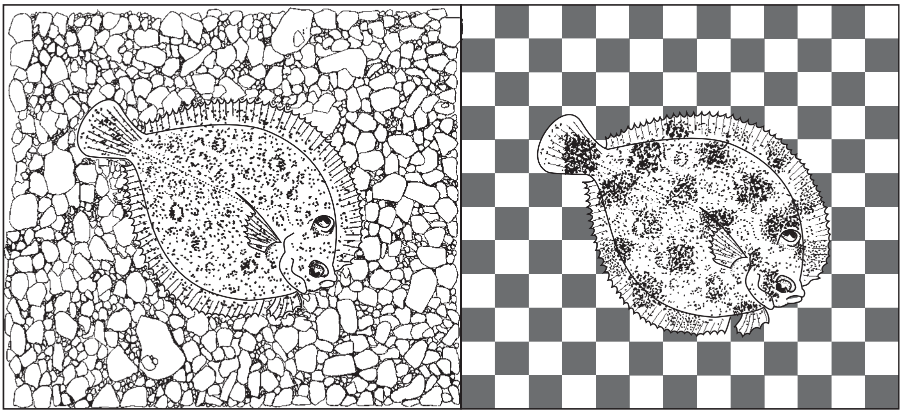


Figure 3.6. Examples of camouflage, showing how a tropical flounder changes its pattern to match the substrate. From photographs in Ramachandran et al. (1996) with permission.

animals sometimes behave so as to enhance their resemblance to their surroundings. For instance, moths that resemble birch bark not only choose birch trees to rest on, they rest so that their stripes are in the same orientation as the black patches on the bark (see Figure 3.18). Flounders, fish that lie flat on the bottom of the sea, provide one remarkable example of how animals can change their appearance to match the substrate (Figure 3.6). Cephalopods (octopus, squids, and cuttlefish) show truly amazing control over not only the color and pattern but the texture of their skin, and the neural and visual control of their elaborate camouflage is beginning to be understood (Hanlon 2007). However, although many details of animal color patterns have long been thought to aid in camouflage, there is surprisingly little experimental evidence for most of these suggestions (Ruxton, Sherratt, and Speed 2004). A recent exception is a demonstration that color patches that break up the outline of a moth's body ("disruptive coloration") do in fact reduce predation by birds compared to the same patches entirely within the body contours (Cuthill et al. 2005).

Far from being cryptic, some animals have what would appear to be the maximum possible contrast with their typical backgrounds. Red rain forest frogs and bright yellow-and-black striped caterpillars seem to be advertising their presence to predators. However, many such warningly colored, or *aposematic,* species sting, prickle, taste bad, or otherwise cause their attackers to reject them. Their bright colors may help predators to learn to avoid attacking them and others like them (see Chapter 6). Contrast with the background is also important in intraspecific communication, as exemplified by the colorful plumage and loud songs of many male birds (see also Section 3.5)

3.4 Signal detection theory

3.4.1 Detecting signals in noise: Theory

In Section 3.3, threshold was mentioned as if it were a definite quantity above which a stimulus is always detected and below which it never is. Even in the best-controlled psychophysical experiment, however, data do not fit this pattern. Observers report detecting a constant stimulus only a proportion of the time. Threshold is calculated as the value detected a fixed proportion of the time, often 75% or 80%. Variation in response to a constant stimulus is thought to be due to inevitable changes in the observer's state, perhaps lapses in attention or spontaneous firing of sensory nerves, and to uncontrollable fluctuations in the stimulus. In addition, data from different observers can vary because people vary in how willing they are to say "it's there" when they are unsure. Thus the idea of an observer with an absolute threshold must be replaced by the idea that a stimulus has a distribution of effects. The observer's problem is to detect that signal against a fluctuating background with which the signal can be confused (noise). An animal's problem in nature is essentially the same: to detect biologically important signals in an environment filled with unimportant stimuli (see Wiley 2006). For both the psychophysical observer and the animal in the field a certain proportion of mistakes is inevitable, and their cost must be kept to a minimum. Signal detection theory quantifies this fundamental tradeoff.

Signal detection theory (Figure 3.7) was originally developed to tell radar operators the best way to decide which blobs to treat as planes on a noisy radar screen. It has been used extensively in the analysis of human psychophysical data (Macmillan and Creelman 2005), but the ideas it embodies apply to any difficult discrimination performed by any creature. Signal detection theory conceptualizes the perceiver as faced with the task of discriminating some signal from a noisy background (which could be another signal). Signal and noise both have a distribution of effects. The

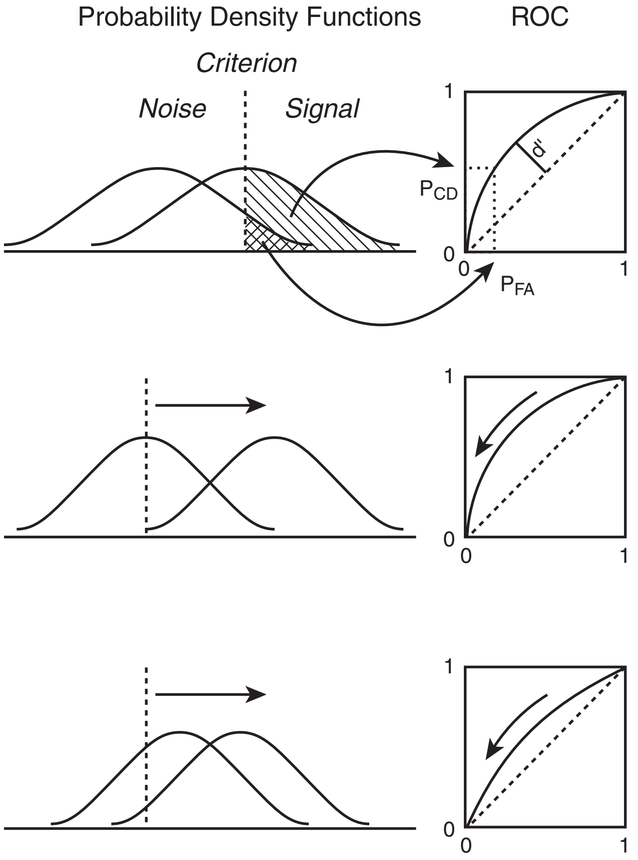


Figure 3.7. The elements of signal detection theory. Hypothetical normal probability distributions of the effect of signal and of noise along some stimulus dimension together with the placement of the criterion for classifying stimuli as "signal" vs. "noise" translate into ROC curves. As the criterion moves from left to right, as shown in the two lower panels, correct detections (CD) and false alarms (FA) move along the ROC curve in the direction of the arrows. As signal and noise become less discriminable, in the bottom panel, performance moves onto an ROC curve with a smaller d.' After Wiley (1994) with permission.

computations are simplest if these distributions are normal with the same variance, as in Figure 3.7. The essential features of these distributions, regardless of their shape, are that *(1)* they overlap, more so the more similar are signal and noise; and *(2)* the value along the stimulus continuum (x-axis) represents the only information about the signal that is available to the perceiver. Thus, many stimuli are inherently ambiguous: the perceiver cannot know whether they represent the noise alone or the signal. All the perceiver can do is to set a decision criterion, a value along the stimulus dimension above which to say "signal" and below which to say "no signal." Once the criterion is set, any of four things can happen: the observer can say "signal" when there is in fact a signal; these responses are termed *correct detections* or *hits*. Inevitably, however, the observer will sometimes say "signal" when there is no signal; such responses are *false alarms*. Saying "no signal" when the signal is in fact absent is a *correct rejection;* "no signal" when a signal is there is a *miss*. Thus there are two kinds of correct responses, and two kinds of errors (Table 3.1). The probability of each is related to the location of the criterion and the overlap between the two distributions as shown in Figure 3.7.

With fixed characteristics of the signal, the background, and the sensory system, correct detections and false alarms change together in a way described by the receiver operating characteristic, or *ROC curve* (Figure 3.7). ROC curves are characterized by their distance from the diagonal that bisects the plot of p(correct detection) versus p(false alarm), represented by the parameter *d′* ("dee prime"). A perceiver with a lower criterion, saying "signal" more often, has more correct detections but necessarily more false alarms (and concomitantly fewer correct rejections) as well. A conservative observer will make few false alarms but concomitantly fewer correct detections. The optimal location of the criterion depends on the relative payoffs for the four possible outcomes described above. For instance, as the payoff for correct detections rises relative to the penalty for false alarms, the criterion should be lower, that is, the observer should respond more often as if the signal is present. The same thing should happen if the observer learns that signals are relatively common. Observers can move onto a ROC curve further from the diagonal, with higher d′ and higher sensitivity, only if the stimuli become more discriminable. This can happen because of changes in the signal, the noise, or the observer's sensory system.

3.4.2 Data

Humans and other species do perform in psychophysical experiments as predicted by signal detection theory. For example, Wright (1972) tested pigeons' ability to discriminate wavelengths in the way depicted in Figure 3.8a. This two-alternative forced-choice experiment was designed to ask the bird whether it perceived both halves of a central pecking key as the same color or as different colors. It pecked a left side key to report

Table 3.1 Possible responses in a signal detection task

		Signal	
		Present	Absent
Response	Yes ("Signal there")	Correct Detection (Hit)	False Alarm
	No ("No signal")	Miss	Correct Rejection

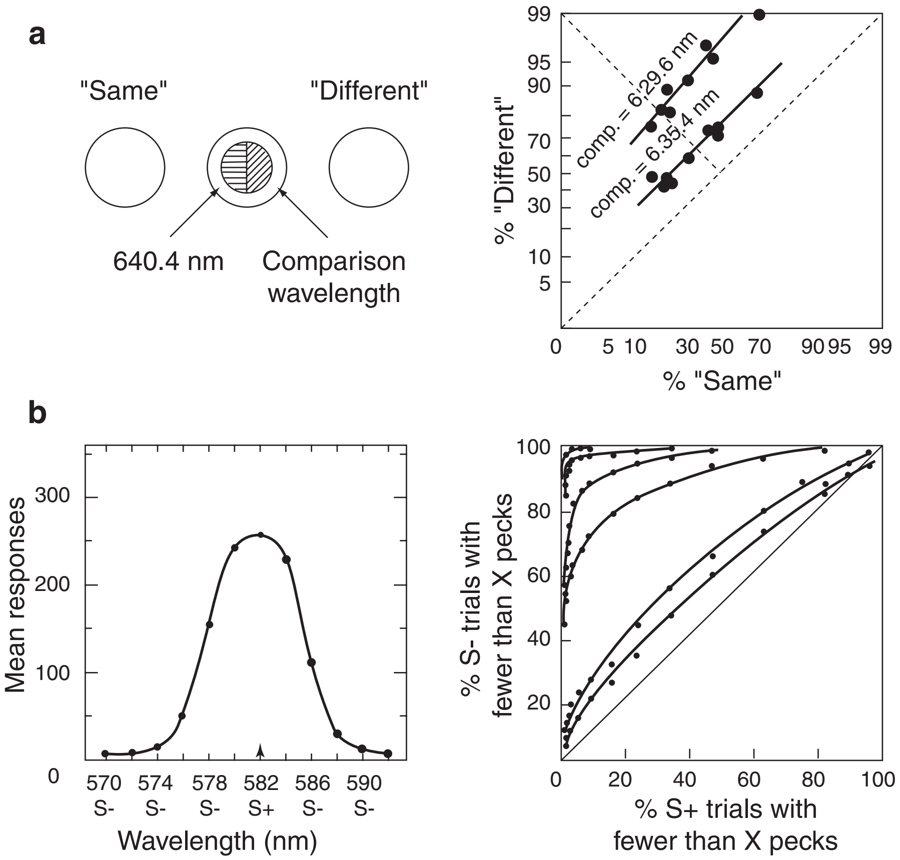


Figure 3.8. a. Method and results of Wright's (1972) experiment on wavelength discrimination in pigeons. The discs are the pecking "keys" referred to in the text. The ROC curves described by the results are plotted as as straight lines on logarithmic coordinates. b. Pigeons' wavelength generalization gradient and derived ROC curves from Blough (1967). Redrawn with permission.

"same" and the right side key to report "different." A bird was occasionally rewarded with food for reporting "same" or "different" correctly. Feedback was always given by briefly turning on a light above the feeder after correct responses but extinguishing all lights in the test chamber after incorrect responses. The bird's criterion for pecking left vs. right was manipulated by varying the probability of reward for correct left vs. right responses. On some sessions it was more profitable to report "same" correctly than it was to report "different," and on other sessions the opposite was true. The pattern of results was exactly as predicted by a signal detection analysis. For each pair of wavelengths, plotting the probability of correctly reporting "different" (i.e., hits) versus the probability of incorrectly reporting "different" (i.e., false alarms) traced out a single ROC curve as the payoffs were varied. For example, when the probability of reinforcement for reporting "different" (pecking the right key) was relatively high, the birds behaved as if adopting a liberal criterion, with a relatively high p(correct detection) accompanied by relatively high p(false alarm). And as indicated in Figure 3.8 a, the more the wavelengths differed, the further from the diagonal was the ROC plot (i.e., the higher the d′).

Wright's procedure for varying the birds' criterion required each bird to complete many trials at each combination of wavelengths and reinforcement probability, but human observers can be asked to apply several criteria simultaneously by reporting the certainty with which choices are made. Responses given with high certainty are assumed to have exceeded a more stringent criterion than those given with lower certainty. Animals can reveal their "certainty" about their choices by how quickly or how much they respond. If the choice keys in a psychophysical experiment are lit for a fixed amount of time on each trial, the number of responses made to the chosen alternative in that time behaves like the human observers' report of subjective certainty. For example, Blough (1967) trained pigeons on a difficult wavelength discrimination. A central pecking key lit up for 30-second trials with one of 13 wavelengths. Pecks at 582 nm were reinforced, but pecks at any of 12 other wavelengths ranging between 570 and 590 nm were never reinforced. The birds' rates of pecking traced out a typical *generalization gradient,* with more pecking to stimuli closest to the positive, or reinforced, stimulus (Figure 3.8b). One way to interpret these data is to say that the lower the rate, the more certain the bird was that the stimulus was not 582 nm. For each nonreinforced stimulus, the proportion of trials with fewer pecks than each of a series of criteria did trace out a ROC curve, just as this notion suggests, with stimuli further from 580 nm giving ROC curves of higher d′ (Figure 3.8b).

3.4.3 Implications for the evolution of animal signals

The examples presented so far have been framed in terms of psychophysical experiments, but signal detection theory applies to any decision whether or not to respond to a signal. The "decision" need not involve performing a learned response for reward. The criterion can represent the threshold for attacking a possible rival or prey item or for displaying to a female. The threshold might be adjusted through evolution or through individual experience. Likewise, evolution and/or experience might adjust the distributions of signal or noise effects, by altering some aspect of the signaler or the sensitivity of the receiver. The payoffs may be in terms of energy wasted, injury risked, food items or mating opportunities gained or lost. Here we consider an example from animal signaling systems. In later chapters we will see how signal detection theory can be applied to other animal decisions (for further discussion and related models see Getty 1995; Sherman, Reeve, and Pfennig 1997; Bradbury and Vehrencamp 1998; Phelps, Rand, and Ryan 2006; Wiley 2006).

Suppose the perceiver is a female bird in the spring, living in an area inhabited not only by males of her own species but by males of another species that look and sound very similar to her species male. Natural selection will have ensured that she is more likely to mate with a male of her own species than with males of other species. To emphasize how signal detection theory applies here, the following discussion refers to the female's decision to mate or not to mate. This means only that the female performs or does not perform some behavior leading to successful copulation and production of young. It does not necessarily mean that she decides in the same way a human observer in a psychophysical experiment decides how to classify a light or a tone. The female's decision mechanism might be as simple as the evolutionarily determined threshold for performing a display that in turn elicits copulation by the male.

The female's problem can be translated into the language of signal detection theory as shown in Figure 3.9 (see also Wiley 2006). Here the signal and noise distributions represent the sensory effects of some male feature or features such as plumage color or song. The "signal" is the distribution from males of the female's own species; "noise" is signals from the other species. The criterion represents the female's threshold for mating with a male, although in fact successful copulation is not usually the result of a single response on the part of either male or female. Correct detections result in viable, fertile offspring, the ultimate evolutionary payoff. False alarms waste reproductive effort. Because many birds lay just one clutch of eggs in a season and may not live long past their first breeding season, incubating eggs and feeding young that do not eventually put their parents' genes into the next generation does represent a considerable cost, putting pressure on females to adopt high criteria. On the other hand, too many missed detections of conspecific males means that the breeding season may pass or all males become mated before the female mates at all, so some false alarms may be worth the risk. In cases where the costs and benefits of each possible outcome can be quantified, the optimal criterion can be derived (see Chapter 14 in Bradbury and Vehrencamp 1998). An informal analysis nevertheless provides two important insights (Wiley 1994).

First, whatever their criterion, females are stuck with at least some false alarms and missed detections unless something reduces the overlap of the signal and noise distributions, that is, moves the female onto an ROC curve of higher d′. This can occur in two ways. The two distributions can stay the same shape while their means move further apart (Figure 3.9). This might represent the case of males of the two species in our example evolving more differentiated songs or displays, a phenomenon referred to as *character displacement*. The female's discrimination will also improve if the distributions become narrower while the means remain the same. This might represent the case of changes in the female's sensory system that, for example, sharpen her sound or color discrimination ability. She might also pay more attention to the parts of the signal that best differentiate the species. The distributions of sensory effects from the males could also sharpen if the males evolve to broadcast their signals more effectively. For example they might sing from more exposed perches so their songs are degraded less before reaching the female.

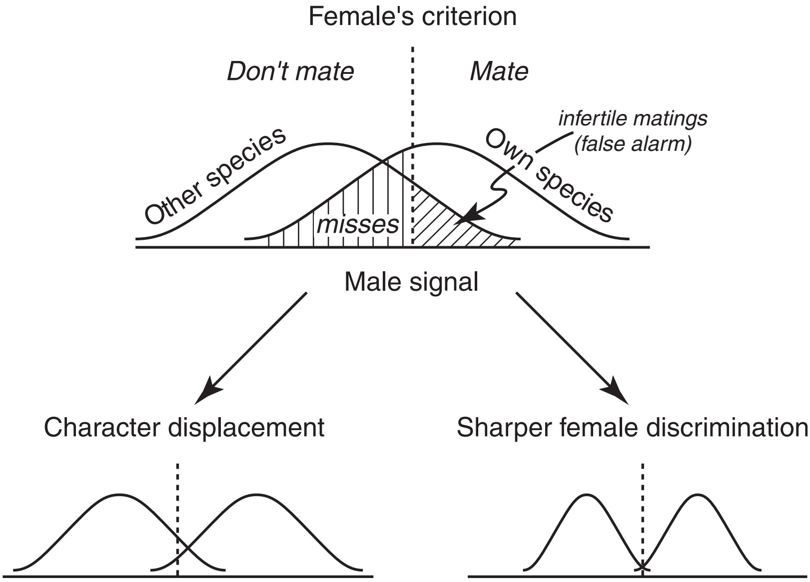


Figure 3.9. Signal detection theory applied to mate choice, showing how false alarms (infertile matings) can be reduced either by males evolving more discriminable characteristics or by females evolving better discrimination.

The second insight afforded by a signal detection analysis of mating signals is that in a situation like that depicted in Figure 3.9, where the signals of two species overlap, the males successful in achieving matings will have a more extreme distribution of signal characteristics than the distribution in the population. That is to say, they will have exaggerated signals, and in fact this is often true (Ryan and Keddy-Hector 1992). As long as the male features that release female sexual behavior are at all similar between species living in a given area (*sympatric* species), the typical payoff matrix for this situation means that females should reject the conspecific males most similar to males of the other species. Therefore the average acceptable male will differ more from males of the other species (or from background noise of whatever sort) than from the average male of the species. If the male characteristics that elicit sexual responses in females are heritable, over generations this process will cause the average male to differ in a more and more extreme way from males of sympatric species and/or from the environmental background.

Exaggerated features elicit greater than normal responses in systems other than sexual behavior. Egg retrieving in the herring gull provides a classic example. An incubating herring gull that sees an egg placed just outside its nest uses its beak and neck to roll the egg into the nest. The Dutch ethologist Baerends and his colleagues (Baerends and Kruijt 1973) presented gulls with pairs of artificial eggs differing in size, color, or speckling and recorded which one of each pair the gulls chose. The preferred size and number of speckles were both greater than the values typical of the study population. The preferred values were combined in a giant, densely speckled egg to create a *supernormal releaser* of retrieval, an egg which the gulls preferred to a normal egg. Comparable effects of supernormality are found in other species of ground nesting birds (Figure 3.10). One might speculate that they appear when selection pressure works to sharpen a discrimination in only one direction. For example, presumably it is important not to retrieve a lot of noneggs. The activity wastes energy (beaks not being very efficient retrieval tools) and extra objects

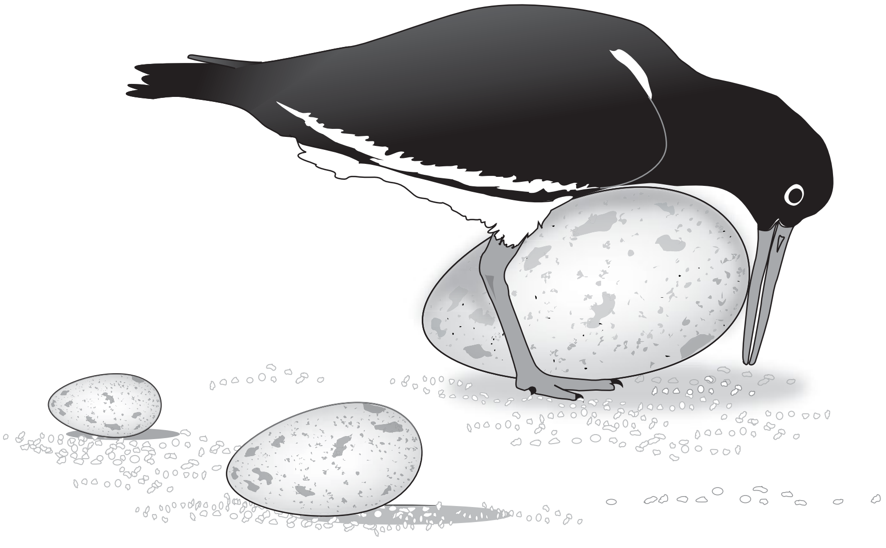


Figure 3.10. Oystercatcher attempting to incubate a supernormal egg. The egg on the left is a normal oystercatcher egg; the one to its right is a herring gull egg. After Tinbergen (1951) with permission.

cluttering the nest mean less room for eggs and chicks. A discrimination in favor of supernormal eggs may indicate that over evolutionary time the typical nesting habitat contained more small, plain, dull than large, colorful, speckly noneggs, leading to a bias in favor of retrieving the largest, most speckly object in sight. An analogous phenomenon in discrimination learning is peak shift (see Chapter 6 and Ghirlanda and Enquist 2003).

3.5 Perception and evolution: Sensory ecology

Some of the most important sensory information animals have to process comes from other animals. Interactions between predators and prey, parents and offspring, males and females both shape and are shaped by the characteristics of sensory systems. Together with the features of the environment that determine the most effective channels for communication, the senses of their conspecifics and predators influence animals' behavior, appearance, and lifestyle. Unrelenting competition to detect the best habitat, food, and mates constantly selects for animals able to make sharp discriminations. The area of behavioral ecology that deals with these issues is sometimes called *sensory ecology*. Studies at the frontiers of sensory ecology combine physics, neuroscience, and molecular phylogeny with behavioral ecology to understand the evolution and present-day distribution of sensory abilities in terms of the stimuli animals are actually processing in nature (e.g., Bradbury and Vehrencamp 1998; Ghazanfar and Santos 2004; Endler and Mielke 2005; Endler et al. 2005; Fleishman, Leal, and Sheehan 2006). The rest of this section discusses two comparatively simple examples of the interrelationship between perception and the evolution of signals which illustrate how experimental and comparative methods, laboratory and field studies, sensory psychology and behavioral ecology can be integrated to shed light on the evolution and normal functioning of animal signaling systems.

3.5.1 Predators and prey

Most animals are subject to two conflicting selection pressures: be inconspicuous to predators but be conspicuous to selected conspecifics. One of the best illustrations of how the tradeoff between these pressures has influenced signals and behavior involves the color patterns and mating behavior of guppies (Endler 1991; Houde 1997). Guppies (*Poecilia reticulata*) are small South American fish that live in clear tropical streams. Mature males sport colored spots and patches that are used in courtship behavior. Male color pattern is heritable and varies in different populations. In experimental tests of the effectiveness of color patches, females are more likely to mate with males that have larger and brighter blue and orange, red, or yellow patches. Thus female choice creates sexual selection pressure for conspicuous coloration. In contrast, predators create selection pressure for cryptic coloration: duller, smaller, color patches, and patterns that match the background.

The effects of predation have been established in several ways. In the field, guppies are found in streams that have different numbers and kinds of visually hunting, diurnal predators, mostly other fish. Males from populations with more predators are more cryptically colored. Prawns are thought to see poorly in the red end of the spectrum. As might therefore be expected, guppies in areas with heavy predation by prawns have more orange than guppies subject to predators with better red-orange vision (Millar, Reznick, Kinnison et al. 2006). Predictions about the effects of predation have been tested directly by establishing guppies from a single genetic background and distribution of color patterns in laboratory "streams" and exposing them to different numbers and kinds of predators. In guppies' natural habitat of forest streams, the intensity and wavelength of light varies with the time of day (Figure 3.2). Visually hunting predators are most active in the middle of the day, but in both the laboratory and the field, guppies engage in more sexual display early and late in the day, that is, in relatively dim light. Taken all together, the transmission characteristics of tropical streams and the visual capabilities of guppies and their most common predators indicate that at the times of day when they are most likely to be courting, guppies' colors are relatively more conspicuous to other guppies than to guppy predators (Endler 1991; Millar et al. 2006).

The foregoing example illustrates how visual conspicuousness and crypticity are literally in the eyes of the beholder. Detailed sensory physiology may be needed to figure out whether color patterns that appear conspicuous or cryptic to us appear that way to the animals that normally view them (for examples see Endler and Mielke 2005; Fleishman, Leal, and Sheehan 2006). A particularly nice example involves camouflage of crab spiders (Thery et al. 2005). Crab spiders make their living sitting on flowers waiting to grab bees or other pollinators that happen by. But by resting in such an exposed position, the spiders make themselves conspicuous to insectivorous birds. Clearly, they should be colored so as to be inconspicuous to both birds and bees, but this is not easy because bees and birds have different color sensitivities (see Box 3.1). Thery and colleagues (2005) collected crab spiders (*Thomisus onustus*) from the yellow centers of white marguerite daisies and measured the relative intensities of wavelengths across the spectrum, including the ultraviolet, reflected by daisy petals and centers and by crab spiders. The daylight reflectance spectra were then related to the color sensitivities of birds (blue tits, typical predators in the French meadows where the spiders were collected) and honeybees. These computations showed that the spiders' color did not contrast sufficiently with the flower centers for them to be detected by either predator or prey. Their contrast with the petals was well above both birds' and bees' thresholds, which presumably selected for spiders to rest in the center. To make matters even more interesting, individuals of this species of crab spider also match their color to pink flowers, and they are similarly of low contrast to both birds and bees on this background as well (Thery and Casas 2002). To human eyes, Australian crab spiders (*T. spectabilis*) are cryptic on white daisies, but from a honeybees' point of view they are highly visible because they reflect much more UV than the daisy petals. Bees are actually attracted to flowers with these UV-reflecting spiders, apparently expressing a general preference for flowers with contrasting markings (Heiling, Herberstein, and Chittka 2003).

3.5.2 Sensory bias and sexual selection: Frog calls and fish tails

Darwin (1871) was the first to discuss an evolutionary puzzle that is still being debated today: why do males of some species have secondary sexual characters so large or conspicuous that they must be detrimental to survival? Natural selection would be expected to mitigate against cumbersome antlers and extraordinarily long brightly colored tails, so why do such exaggerated characters persist? Darwin's answer was that such ornaments evolve because females prefer them: the force of sexual selection outweighs the forces of natural selection. Roughly speaking, sexual selection occurs due to greater reproductive success of individuals preferred as mates by the opposite sex; in most cases females do the choosing, driving appearance and behavior of males. A central question in this area is "What is the evolutionary cause of the observed patterns of female choice, in particular, females' preference in many species for exaggerated male characters?" There are several answers. As explained next, each may be correct for some situations (Andersson 1994; Maynard Smith and Harper 2003; Searcy and Nowicki 2005).

It is not particularly problematic why females may prefer male characters correlated with large size, good health, or—in species with biparental care—ability to help rear the young. For example, growing bright glossy feathers may be possible only if you can get enough of the right foods to eat and resist diseases and parasites. Such characters may signal that the male has "good genes" that allow him to be strong and healthy and/or provide resources for a female and her offspring. Genes for preferring males that are better fathers would spread because daughters of females with these genes would inherit preference for better fathers, sons would inherit the genes for being better fathers, and by definition better fathers have more offspring than poor ones. A preferred character of this sort might become exaggerated through evolution as discussed in Section 3.4.3, but it and the females' response to it are selected because it indicates male quality.

The "runaway" hypothesis of sexual signal evolution specifically accounts for signals that seem to have no intrinsic relationship to male quality. It is essentially Darwin's suggestion buttressed by mathematical modeling. Informally stated, if at some stage in evolution females by chance preferred an arbitrary male character, females with the preference and males with the character could come to dominate the gene pool, in a runaway positive feedback process. On this scenario, the female preference and the male character evolved together, and the preferred male character need not be correlated with male quality.

But what gets selection on such a character started in the first place? One prominent suggestion is that preexisting features of females' sensory systems or perceptual preferences make such characters especially attractive, a suggestion known as the sensory bias hypothesis (Ryan 1994; for discussion of the many different terms and ideas in this area see Endler and Basolo 1998). Some kind of arbitrary bias is needed to get runaway selection started, but the sensory bias theory has been thought to make at least two unique predictions (Fuller, Houle, and Travis 2005; Searcy and Nowicki 2005). First, female sexual preferences evolved before male characters. This possibility can be tested with comparative behavioral data and phylogenies. Second, a preference expressed in a sexual context may have a function in another context such as feeding or predator avoidance. For instance, male lizards of the species *Anolis auratus* start their sexual display with a rapid up and down motion of the head (Fleishman 1988). Sudden motion attracts attention in many contexts, and for good reason, as it could indicate a live prey item or an approaching predator. The sexual display of the male water mite *Neumania papillator* includes waving his appendages in a way that mimics the motion of prey items, and in fact hungry females are more likely than sated ones to respond to displaying males (Proctor 1992). The strong attraction of both male and female guppies to orange fruits suggests that the orange spots of male guppies similarly exploit a feeding preference (Rodd et al. 2002; but see Millar et al. 2006). By implication, in these cases responsiveness evolved first in the nonsexual context and males have been selected to exploit it in the sexual context. Cladistic analysis (Chapter 2) has supported this conclusion for water mites.

In all the foregoing examples the chief evidence that a more general preference is reflected in sexual signaling is the observation that all members of the species show it. For instance, whether breeding or not both male and female guppies are attracted to orange fruits (Rodd et al. 2002). When instead phylogenetic inference is the main support for a hypothesized preexisting bias, conclusions are very much dependent on the number of species used to collect behavioral data and to construct the phylogeny on which conclusions about signal evolution are based. This important point is illustrated very well by two of the original candidates for signals evolved through sensory bias. One is the swordlike extension on the tails of male swordtail fish (Ryan and Rand 1995; for another example see Garcia and Ramirez 2005). Female swordtails prefer long swords over short ones (Basolo 1990a; Basolo 1990b). Platyfish are a group of swordless species that share a common ancestor with swordtails (Figure 3.11), and females of a swordless platyfish species prefer males with swords as sensory bias predicts. Now the question for a phylogenetic analysis is whether the most recent common ancestor of swordtails and platyfish had a sword or not. The best phylogeny available when Basolo made her discovery (Figure 3.11top), indicates that swordlessness is ancestral, and therefore preference for swords must have evolved before swords. However, a later phylogeny based more heavily on similarities in DNA (Figure 3.11bottom) seems to indicate that swords were ancestral and have been gained and lost several times within the swordtail-platyfish group (Meyer, Morrissey, and Schartl 1994). But even newer behavioral data reveals that in a species

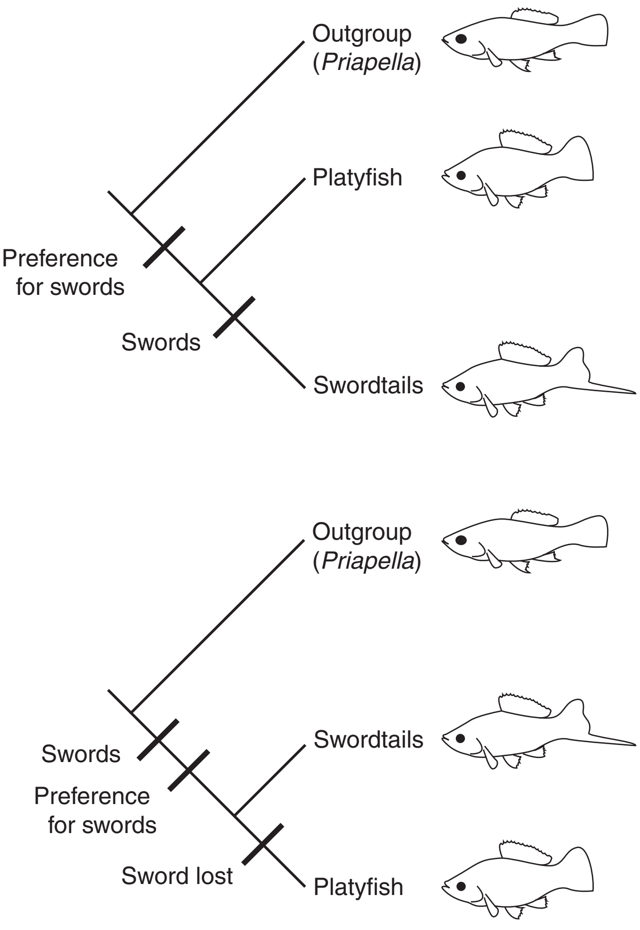


Figure 3.11. Possible alternative pathways for the evolution of swords and sword preference in swordtails and platyfish. The phylogenies are simplified, since each branch actually contains numerous species. Adapted from Basolo (1995a) with permission.

in the outgroup for this phylogeny, that is, the closest relative of both swordtails and platyfish, females also prefer males with swords (Basolo 1995b; but see Basolo 2002), indicating that preference for swords predated any evolution of swords.

The call of the male túngara frog, *Physalaemus pustulosus,* is another male mating signal hypothesized to have evolved through exploiting the sensory bias of females (Ryan and Rand 1993). In this case tests of the sensory bias hypothesis have included physiological studies of the frogs' auditory system as well as behavior and phylogeny. The call of the male túngara frog contains a whine followed by a number of lower-pitched chucks. The whine is necessary and sufficient for mate recognition, but the addition of chucks enhances the attractiveness of the call to females in choice tests in the laboratory. Chucks contain predominantly the frequencies to which the female frog's inner ear is most sensitive, suggesting that chucks might be quite stimulating to females generally, even though males of closely related species do not add chucks to their calls. This proved to be the case with the first set of species studied. Females of the closely related species *P. coloradorum* responded more to *P. coloradorum* calls with added chucks than to unaltered calls. Thus they have a preference for calls with chucks, which they normally do not express because males of their species do not chuck. Phylogenetic analysis based on characters other than male mating calls initially indicated that the chucks are recently evolved, as the sensory bias hypothesis requires (Ryan and Rand 1993). Accordingly, the frog calls became a key example of signal evolution through sensory bias. However, when more species are included in both the phylogeny and the tests of auditory sensitivity and female preference, the pattern is inconsistent with preexisting sensory bias. Instead, female preference and male calls seem to have coevolved, implying that some degree of central decision making is involved in the females' choice (Ron 2008; see also Phelps, Rand, and Ryan 2006). Although this tale may not be all told yet, it illustrates very well the much more general principle that conclusions about the evolution of cognition and/or the role of cognition in evolution depend on testing plenty of species and having good information about the relationships among them. The latter, in particular, depends heavily on how many and which species are included in the analysis (see Ron 2008).

3.6 Search and attention

At any given moment, most of the surrounding environment is irrelevant for current behavior. For example, as you read this book, you may be drinking a cup of coffee and playing your stereo, but neither the taste of coffee nor the sound of music is relevant for the task at hand. For some species, like the *Bembyx* moth, the problem of selecting what parts of the world to respond to has been solved by the evolution of specialized sensory channels and stimulus coding mechanisms ensuring that the moth senses only the few things in the world that matter for survival and reproduction. But such reliable coding limits flexibility. Animals like birds, monkeys, and human beings that can perceive a wide range of stimuli from several sensory modalities need a way to ensure that, for example, they switch appropriately from looking for food at one moment to looking for a safe refuge at another. Attention is one process that does this selecting. Motivational processes may play a role too, for example by changing thresholds for responding to relevant stimuli with physiological state.

Concentrating on reading while doing other things illustrates how attention is used as a filter, deployed in this case in a top-down manner (i.e., through some internal decision process). But attention doesn't necessarily filter out all but one set of cues. A door slamming, or someone calling your name can grab attention (an example of a bottom-up or externally driven switch of attention). In these examples, attention has the beneficial effect of ensuring that the important things of the moment are processed best. But attention also has a cost: if we actually listen to the radio while reading, we'll get less out of the reading (and vice versa) than if we do one thing at a time. Why attention is limited is a much debated theoretical question. Obviously it sometimes solves the problem of animals not being able to do two physically incompatible things at once, such as search for food and watch for predators, but this does not explain why it should not be possible, for example, to search for two kinds of food as efficiently as for one or to read while listening to the radio. This property of attention may reflect basic limitations on the size of the brain due to the metabolic costs of neural tissue (Dukas 2004). Traditional psychological theorizing similarly assumed a limitation on perceptual processing resources or a bottleneck in more central processing, but contemporary theorizing has identified alternative possible mechanisms, some of them better specified (Luck and Vevera 2002). But rather than advancing any general theory, research on attention in nonhuman species has primarily aimed to establish effects similar to those found in people (Section 3.6) and show how attention plays a role in ecologically relevant behavior (Section 3.7).

3.6.1 Visual search: The basics

Much data and theory on attention in humans is based on research with visual stimuli (Luck and Vevera 2002). Comparable experiments with highly visual animals, primarily monkeys and birds, indicate that basic attentional processes are shared across species (reviews in Blough 2001; Zentall 2005b; Blough 2006). Clearly, however, the important things in life are sometimes defined by sound, smell, or other nonvisual stimuli. For example, a father penguin returning to the colony with food needs to be able to pick out his mate's or baby's calls from those of hundreds of others (Aubin and Jouventin 2002). Such *auditory scene analysis* has been extensively studied in the context of animal vocal communication (Hulse 2002). It is also important in understanding how bats distinguish prey-generated echoes from background noise (Moss and Surlykke 2001). However, because the most detailed analyses of animal attentional processes have addressed visual attention, that will be the focus here.

In visual search tasks (Schiffrin 1988; Treisman 1988) as the name implies, the subject searches for something by looking for it. The thing being searched for is referred to as the *target*. It is embedded among other items, the *distractors*. Figure 3.12a shows a typical example for a human subject, a target X among distracting Os, and one that might confront a visual granivorous predator, a black seed among white pebbles. No one reading this book would fail to find the X or the seed in Figure 3.12a, but suppose the figure had been flashed for a fraction of a second or the distractors were much more similar to the target, say Ys instead of Os surrounding the target X. Now the results would start to be interesting. Under these sorts of conditions, with limited viewing time or high similarity between target and distractors, subjects may make mistakes and/or take longer to find the target.

In Figure 3.12a, the target X seems to "pop out" from the background of Os. The same would be true if the target were a yellow X among red Xs or a moving dot among stationary ones. The pop out effect is evident in data from visual search tasks

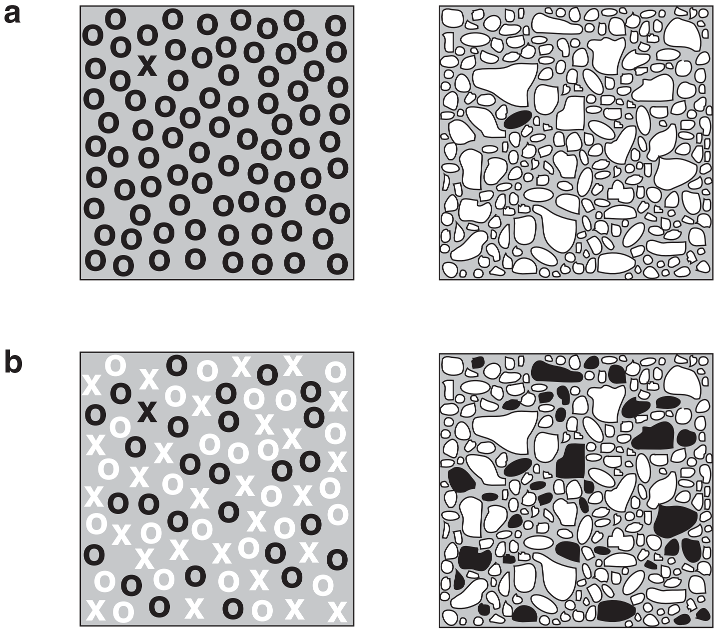


Figure 3.12. Typical stimuli for visual search experiments. a. Targets defined by a difference in one feature (shape or color) "pop out" from the background. b. Conjunctively defined targets, the black X and the black grain, take longer to find. Panels on the right adapted from Dawkins (1971) with permission.

in the fact that with such displays reaction time (latency to detect the target) increases only slightly with the number of distractors (Figure 3.13). In contrast, when the target is defined by the conjunction of two features, for example a black X or among black Os together with white Xs and Os (Figure 3.12b), reaction time increases sharply with the number of distractors. One interpretation of this pattern of data is that when target and distractors differ in just one feature, the objects in the display are processed in parallel, that is, all at the same time. When the target is defined by a conjunction of features, the items have to be processed serially, that is, one by one. With conjunctive targets, the times taken to decide "no, the target is not there" support this interpretation. Every item in the display must be mentally inspected in order to decide the target is absent. It will take twice as long on average to say (correctly) "No target" than to locate the target (Figure 3.13). The fact that the functions relating reaction time to number of distractors are straight lines indicates that processing each additional item takes a constant amount of time (Treisman and Gelade 1980).

3.6.2 Feature integration theory

Treisman's (1988, 1999) interpretation of results like those just described is that elementary features of objects such as shape, color, and motion are registered automatically without needing attention (preattentively). Identifying visual objects consisting of a conjunction of features requires that the object's location in space become the focus of attention and the features perceived there be integrated. Some of the evidence in support of Treisman's feature integration theory comes from experiments in which subjects are briefly shown a circular display of colored letters and asked to

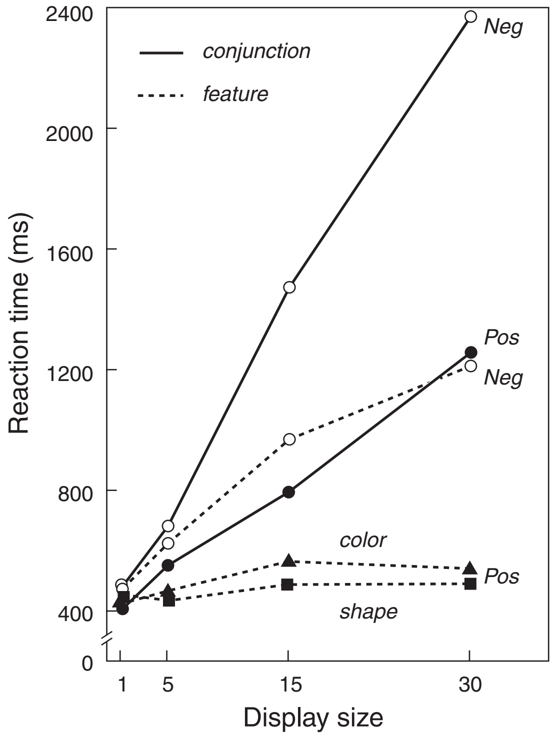


Figure 3.13. Human subjects' latencies to respond correctly in visual search experiments with a target defined by a single feature or a conjunction of features as a function of display size. On positive trials (Pos) the target was present; it was absent on negative (Neg) trials. Redrawn from Treisman and Gelade (1980) with permission.

report the color, the shape, or both the color and shape of the letter in one location. The probability of correctly reporting the conjunction of features is predicted almost perfectly by the probabilities of correctly reporting color and shape separately (Treisman 1988). This pattern of data is consistent with the notion that the object's features are first processed independently rather than as a unit. Moreover, identifying a conjunctive target is strongly associated with reporting its location correctly, as if objects are perceived as a spatial conjunction of independently processed features.

Another way to demonstrate the processes in feature integration is texture segregation. The idea behind texture segregation is that a cluster of identical objects is perceived as a distinct object in itself. As can be seen in Figure 3.14, the distinction between elemental and conjunctive targets is just as evident here as with individual targets: areas defined by a difference in one element, such as a cluster of white objects among black ones, pop out. Areas defined by a conjunction of elements, such as a cluster of white squares and black circles among white circles and black squares, take time to detect. Data from both humans and pigeons support this conclusion (Treisman and Gelade 1980; Cook 2001b).

In the experiments with pigeons (see Cook 2001b; Cook 1992a), birds were trained to peck at displays on a video monitor surrounded by an array of infrared emitters and detectors. This "touch frame" was positioned so that when the bird pecked at the TV screen its beak broke two infrared beams crossing the screen at right angles, and information about the location pecked was transmitted to the computer controlling the stimuli and reinforcers. The screen was covered with rows of small shapes, with one square about a quarter of the screen's area having different shapes from the rest

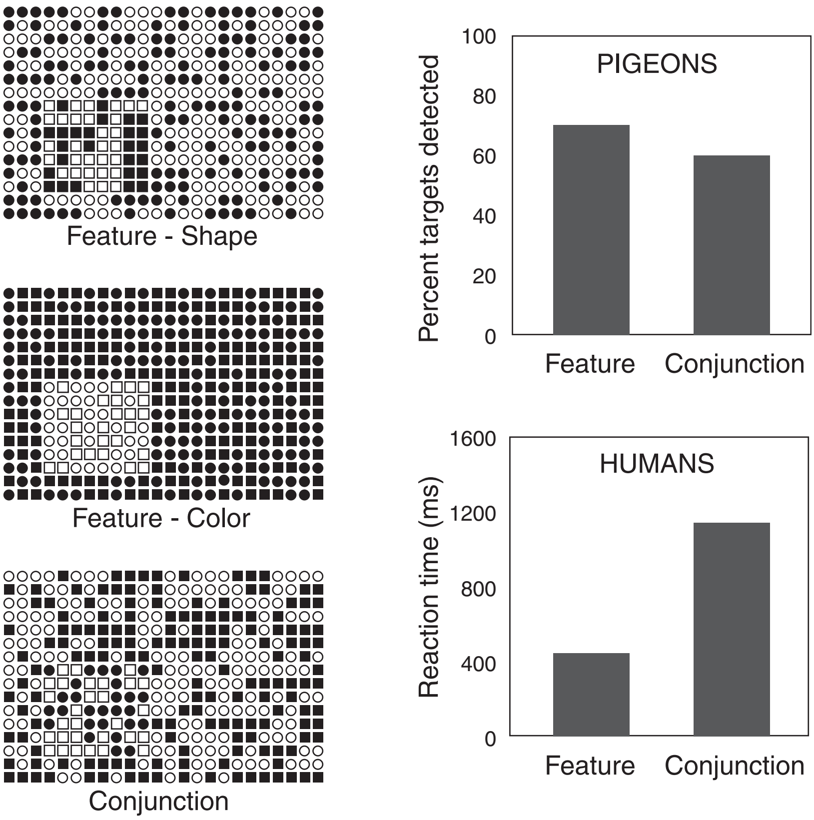


Figure 3.14. Stimuli used to study texture segregation by pigeons and humans and both species' performance with simple ("feature") and conjunctive targets. Data from Cook (1992b); stimuli reproduced from the same article with permission.

(Figure 3.14). The birds were reinforced with food for pecking five times anywhere on this rectangle; one peck elsewhere caused the screen to go dark and postponed the next trial. The pigeons were trained at first with a relatively small number of different small shapes and colors defining the target rectangle and just a few target positions, but they continued to perform well above chance when novel shapes, colors, and positions were introduced. These data alone suggest that, like humans, the pigeons perceived the cluster of distinctive items as "an object" and that they had learned "peck the object," not "peck the training items." Most importantly, targets defined by a difference in a single feature were consistently detected more accurately than targets defined by a conjunction of features. Cook (1992b) tested humans with the same displays as the pigeons. The pattern of results was the same, except that whereas the pigeons showed differences mainly in accuracy of detecting the target areas, people showed differences in reaction time (see Figure 3.14). Nevertheless, these data compellingly indicate that at least this one animal species, evolutionarily and neurologically very different from us, shares the same kind of elemental processing in the early stages of vision (review in Blough and Blough 1997; Blough 2001).

Feature integration can be contrasted with the Gestalt approach to perception, in which perception of the whole is primary and analysis into parts comes later. It also contrasts with the influential approach of J. J. Gibson (1979), which emphasizes the importance of ecologically relevant wholes. For instance, the spatial structure of the environment is immediately evident in the way objects move relative to each other when the observer moves: nearby objects move across the visual field faster than those farther away. The contrast between elemental and holistic approaches pervades theoretical debates about many cognitive processes. Feature integration theory assumes a modular organization of perception in that there is a separate module for processing each stimulus dimension. In evolution, modular organization would permit the ability to process additional dimensions to be added onto an initially simple perceptual system. Similarly, in a modular system the ability to process a feature of particular importance for a given species can be fine-tuned without affecting processing of other features.

3.6.3 Attention in visual search.

In experiments like those just described, visual search is used to test focused attention, that is, the subject searches for one thing at a time. The question being investigated is how the distractors in the visual display do just what their name implies, namely distract the subject from finding the target as rapidly and accurately as possible. If target and distractors are very different, the popout effect occurs and the number of distractors does not matter. But with increasing similarity between target and distractors, even when the subject searches for just one type of target reaction times increase (or accuracy decreases) as the number of distractors (the *display size*) or the similarity of the distractors to the target increases. The data from search for conjunctive targets in Figure 3.13 illustrate effects of display size in humans. Figure 3.15 illustrates comparable effects of similarity and display size for pigeons.

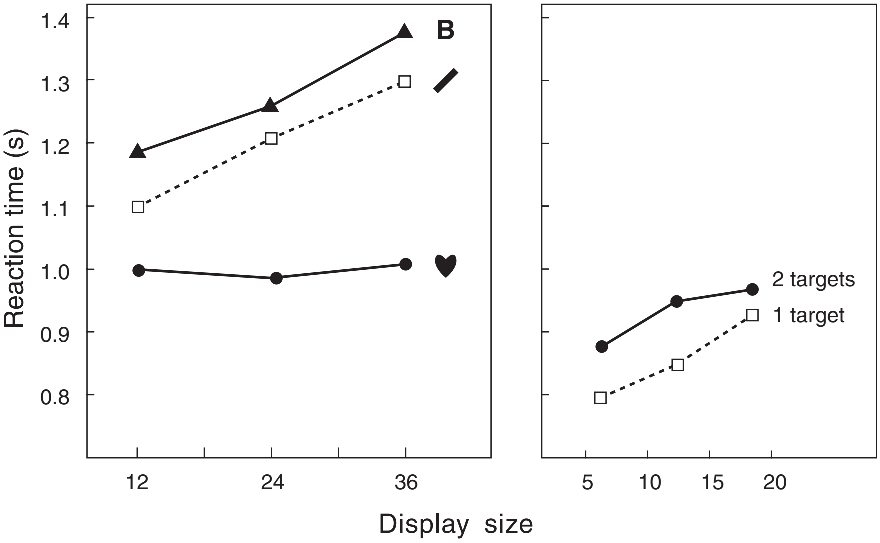


Figure 3.15. Effects of display size (number of items) and target-distractor similarity (left) or memory set size (right) on visual search in pigeons, as measured by time taken to locate the target (reaction time). Left panel redrawn from P. Blough (1992) with permission; the distractors were standard alphanumeric characters, hence the heart shape was the least similar and "popped out." Right panel, one pigeon's data from P. Blough (1989), redrawn with permission.

Figure 3.15 also illustrates the effects of number of possible targets used in a series of trials, the memory set size. In human subjects, too, search slows as the number of potential targets increases. Subjects searching for just one sort of target are like specialist foragers, animals that eat only one kind of thing, whereas subjects for which targets are mixed unpredictably are like generalists, foragers that can eat several kinds of prey. The decrease in performance with a larger memory set size is a cost of being a generalist. If the targets were food items, the benefit to generalists of being able to eat more of what they encounter might have to be traded off against this cost. However, the detrimental effect of memory set size diminishes with extended practice. That is, search becomes automatized as if attention is automatically drawn to items that have frequently been attended to (Schiffrin 1988). With pigeons, too, the effect of display size on search accuracy disappears after extended training, but only with a comparatively small set of potential targets (Vreven and Blough 1998). These findings suggest that generalizing might not have a cost in the wild once animals are familiar with all available items.

The effect of memory set size means that a given target is found more quickly or accurately when it is the only one presented over a series of trials than when it is unpredictably mixed with one or more other targets. Finding one target of a given type *primes* attention to targets of that type. Priming is thought of as a transitory activation or facilitation of processing of the target's features. Priming can occur either sequentially as just described, or associatively. In associative priming, performance is facilitated by presenting a cue that has been associated with the target, either just before or during presentation of the target. For example, in a further part of the study whose results are displayed in Figure 3.15, distinctive borders were added to the stimulus displays. Black and white were paired with A and L, respectively; a striped border, paired equally often with A and L, served as an ambiguous cue (P. Blough 1989; D.Blough 1991). Performance with each letter was better when it was cued than otherwise. If each target is paired consistently with a particular distractor, the distractors themselves may serve as associative priming cues (Blough 1993a).

Priming seems not only to facilitate processing of the primed target, but to inhibit processing of unprimed targets. In P. Blough's (1989) experiments, performance on occasional test trials in which A appeared when L was cued or vice versa was worse than on trials with the ambiguous cue. Pigeons can also be primed to attend to particular areas of a display (Blough 1993b). These data on priming seem to suggest that if foraging is like visual search for prey scattered on a substrate of distractors, as Figure 3.12 was made to suggest, any sources of information about the identity of the prey aid search (Blough 1993a). These include what prey have been found recently (sequential priming), where they have been found (priming by locations), and what substrate they were found on (associative priming). It is not yet clear, however, whether these different sources of priming all work in the same way. When sequential and associative priming are combined, they do not always have the strictly additive effect that would be expected if both enhance the same attentional process (Kamil and Bond 2006).

For animals foraging in the wild, as we see in Chapter 11, what matters is not success or speed on any single trial but overall rate of food intake. A nice demonstration of how attentional priming translates into this currency was a study in which bluejays were trained to search on video displays for two simulated prey items, a brown horizontal bar and a white vertical ellipse in mixtures of different sized brown horizontal bars and white vertical ellipses (Dukas and Kamil 2001). The bird began a trial by pecking a "start" circle surrounding an image of one or both of the possible "prey." A single image reliably cued the item to be found in the upcoming display, presumably allowing the bird to focus its attention on items of the cued color, whereas a double image was an ambiguous cue to item type. As soon as a bird pecked a target once, it received half a mealworm and 3 seconds later the signal for the next trial, whereas pecking a distractor delayed the next trial for 15 seconds. This contingency meant that speed and accuracy at pecking the targets would increase the rate of food intake. Consistent with sequential and/or associative priming, the number of mealworms obtained per minute increased by about 50% when the upcoming prey image was signaled.

3.7 Attention and foraging: The behavioral ecology of attention

3.7.1 Search images

By comparing the kinds of insects birds brought to their young with the kinds available in the trees where the birds foraged, Luc Tinbergen (1960), brother of the more famous Niko referred to elsewhere in this book, discovered that insects are not preyed on when they first appear in the environment. Instead, a new prey type such as a freshly hatching species of caterpillar will suddenly begin to be taken when its abundance increases. This sudden increase in predation, Tinbergen suggested, occurs because predators adopt a specific searching image for that prey type after a few chance encounters. "The birds perform a highly selective sieving operation on the stimuli reaching the retina" (Tinbergen, 1960, 333). Described in this way, adopting a searching image (or *search image*) sounds like an attentional process. Recent experiments have supported this conclusion.

The idea that animals might search selectively, ignoring items that do not match a mental representation of desired prey, is appealing because it agrees so well with introspection. Most people have had the experience of not seeing what is right in front of their noses. Indeed, one of the earliest references to search images in animal behavior is von Uexküll's (1934/1957) description of looking for a familiar earthenware water jug and not seeing the glass one that had replaced it (Figure 3.16).

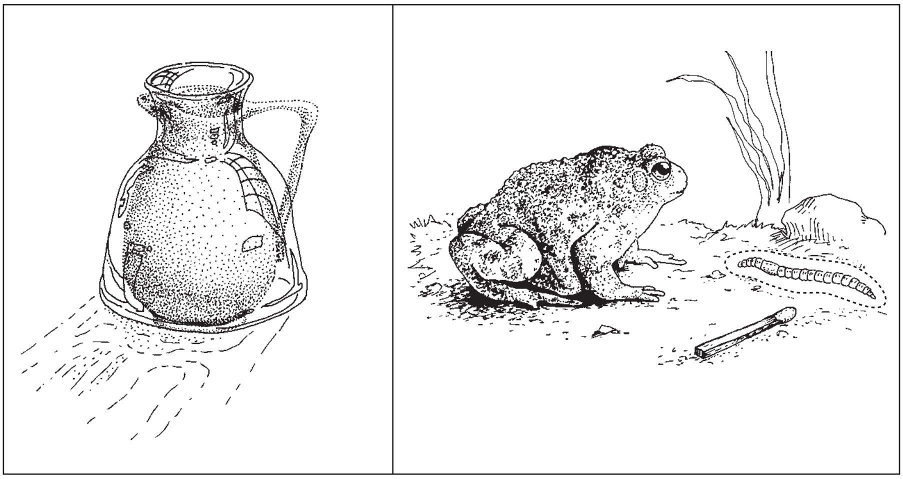


Figure 3.16. Von Uexküll's depiction of his own search image of an earthen water jug and of a frog's search image of a worm. After von Uexküll (1934/1957) with permission.

Animals, too, von Uexkull suggested, could have a mental image of a prey item that enhances their ability to detect matching items and interferes with detecting others (Figure 3.16). It has generally been assumed that an animal can have only one search image at a time, that is, the search image enhances predation on one cryptic prey type while temporarily inhibiting detection of other types. Crypticity is important because search images are assumed to be useful only for prey that are difficult to find in the first place.

By themselves, Tinbergen's data can be explained in a number of ways. Runs of the same type of prey can be explained by the birds repeatedly visiting the same patch of habitat. If the birds were relatively young, they could have been learning that particular insects were suitable as prey or where or how to hunt for them (Dawkins 1971). Learning the characteristics of novel prey in the first place is not the same as selectively attending to a known prey type. Therefore, most recent experiments on search images have varied the abundance and/or crypticity of items that are familiar to the animals being tested. For example, Bond (1983; Langley et al. 1996) studied pigeons searching for two kinds of grains, black gram and wheat, scattered over multicolored gravel. Because the grains were the same color as some pieces of gravel, they were more difficult for the birds to detect on this background than on a plain gray one. After the birds were familiar with feeding on these grains on the gravel backgrounds, the relative proportions of black gram and wheat were varied randomly between 100% black gram and 100% wheat. The birds behaved as if adopting a search image for the more frequent type, taking proportionately more of it rather than matching the proportion taken to the proportion available (Figure 3.17). However, pigeons do match the proportion taken to the proportion available when the prey items are conspicuous, showing that crypticity is important, not just variations in relative proportion (Langley 1996).

One way to find more prey that are difficult to see is to search more slowly, spending longer scanning each section of the substrate (Gendron and Staddon 1983; Guilford and Dawkins 1987). A tradeoff between speed and accuracy in performing difficult discriminations is common to many species, including honeybees (Dyer and Chittka 2004). Reaction time is a good index of the amount of mental processing a task requires, even when it is performed very accurately (see Blough 2006). In the present example, there is an optimal speed-accuracy tradeoff for each

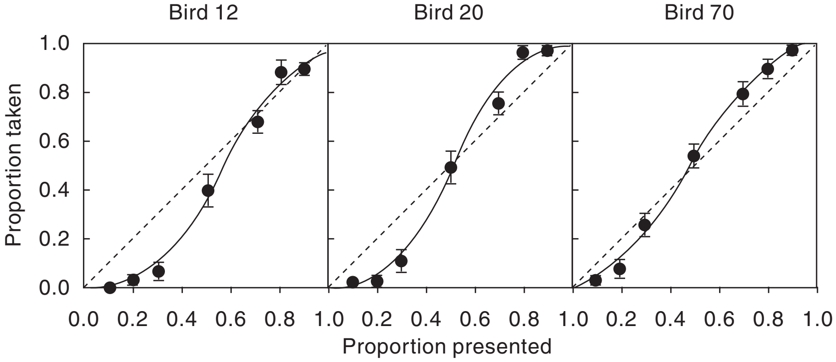


Figure 3.17. Proportion of cryptic grains of one type taken by each of three pigeons as a function of its proportion in a mixture of two types of cryptic grains in the study by Bond (1983). Redrawn with permission.

degree of crypticity that balances the potential benefit of encountering more prey by searching faster against the cost of missing cryptic items by searching too fast (Gendron and Staddon 1983).

The search rate hypothesis predicts that a predator searching slowly should detect all equally cryptic prey equally well. In contrast, an animal with a search image should take one type and ignore the other, even if both types are equally cryptic. Figure 3.17 shows that the two grains used were equally cryptic because when equal numbers were presented (proportion presented = 50%), equal numbers were taken. However, contrary to the search rate hypothesis, the proportion taken did not equal the proportion presented under all conditions. Disproportionate predation on the more abundant type implies that the birds were using a search image for the more frequently encountered grain. This does not mean, however, that animals faced with difficult discriminations in nature might not also search more slowly.

Allowing an animal to search freely for prey items as was done in these studies has some drawbacks as an experimental technique. The animal rather than the experimenter controls the rate and sequence of encounters, and the relative proportion of different items changes as the food depletes. To test the effect of recent experience on choice or detectability of prey it is necessary to present a standard test after differing experiences (Chapter 4). One way to do this is to present prey items one at a time. For example, Pietrewicz and Kamil (1981) tested blue jays (*Cyanocitta cristata*) in an operant task in which they pecked at slides showing two species of moths (blue jays' natural prey items) resting against tree trunks on which they were cryptic. The birds were rewarded with mealworms for indicating correctly that a moth was present. If no moth was present, pecking a central "moving on" key led to the next trial. These pecks generally had longer latencies than pecks to slides with a moth, as if the birds used exhaustive serial search to decide no moth was present. The critical data came from comparing performance in trials following runs of moths of the same type with performance in mixed trials with both species (Figure 3.18). Performance improved within runs as compared to mixed trials. Notably, the birds' accuracy at detecting the absence of a moth improved as well as their accuracy at detecting the presence of a moth, consistent with the notion that attention enhances detection of attended features. These data suggest that the bluejays had a search image for the moth species they had encountered most recently. Because the moths were depicted as they would appear in nature, one species on birch tree trunks and the other on oak trunks, associative priming may have been operating in addition to the sequential priming evident Figure 3.18.

When multiple kinds of prey items can be found on the same substrate, priming presumably occurs when several of the same type are found in succession by chance. Experiments in which pigeons search for grains among gravel have been used to analyze this situation (Reid and Shettleworth 1992; Langley 1996; Langley et al. 1996). Pamela Reid (Reid and Shettleworth 1992) used wheat dyed yellow, green, or brown on a background of green and brown gravel. A free search experiment similar to Bond's established that brown and green were equally cryptic whereas yellow grains were highly conspicuous to the pigeons. To control the birds' experience, Reid then used the apparatus shown in Figure 3.19. Small plaques of gravel, each holding one or two grains, were presented one at a time, and the birds were allowed a single peck at each one. In a run of green or brown after a run of conspicuous yellow grains, the birds' accuracy gradually increased, consistent with their forming a search image for the new cryptic type, just as when they searched freely for grains. However, after a switch from a run of one cryptic type to a run of the other, the birds performed just as

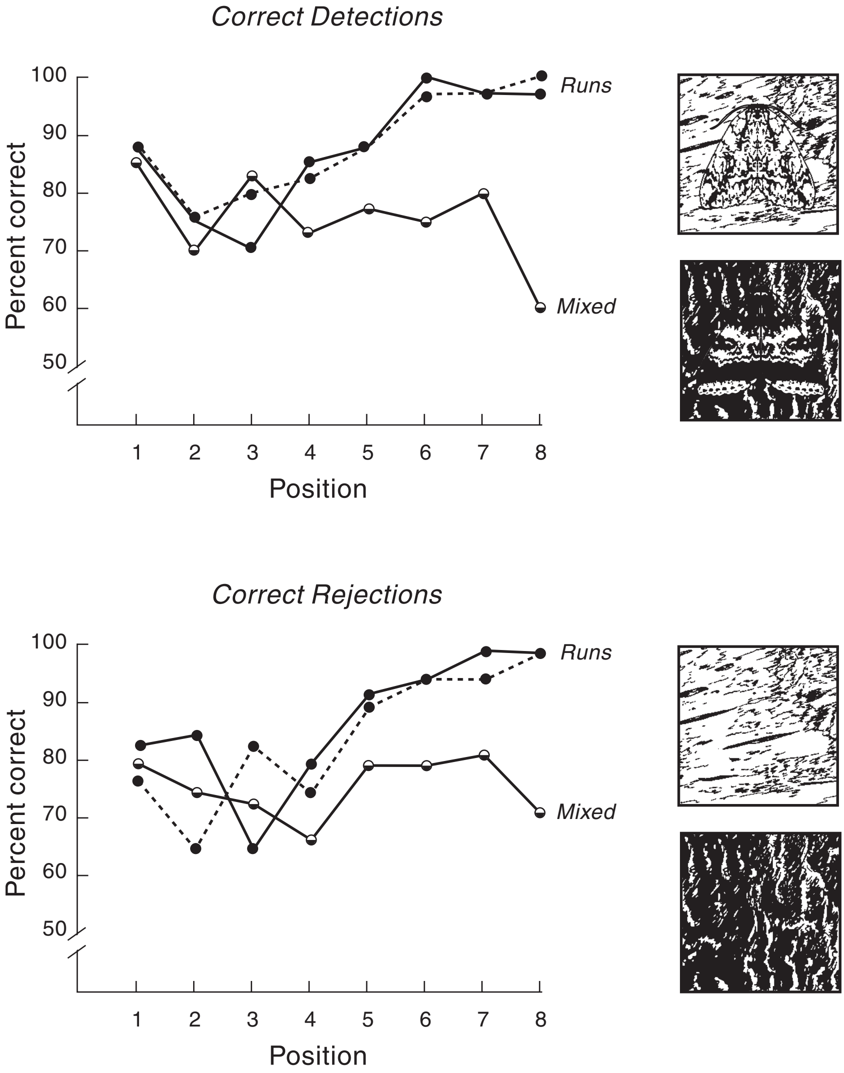


Figure 3.18. Performance of bluejays reinforced for reporting the presence (top panel) or absence (lower panel) of moths in slide images like those on the right in runs of the same moth species or trials with a mixture of two species. Adapted from Pietrewicz and Kamil (1981) with permission.

well as if they had a single cryptic type all along (Figure 3.19). This seems to mean that the birds' "search image" includes some feature distinguishing grains in general from gravel, perhaps shape or texture. Nevertheless, when Reid's pigeons had a choice between brown and green grains, the two cryptic types, after a run of one of them, they tended to choose the color they had just been having. This was not just a general preference for what they had been eating most recently, because the effect depended on the grains being cryptic. Thus the "search image" also seems to include information about the grain's color.

These results naturally lend themselves to interpretation in terms of feature detection and priming. Easy detection of the conspicuous yellow grains is an instance of the popout effect: the target (the grain) differs from the distractors (the bits of gravel) in a

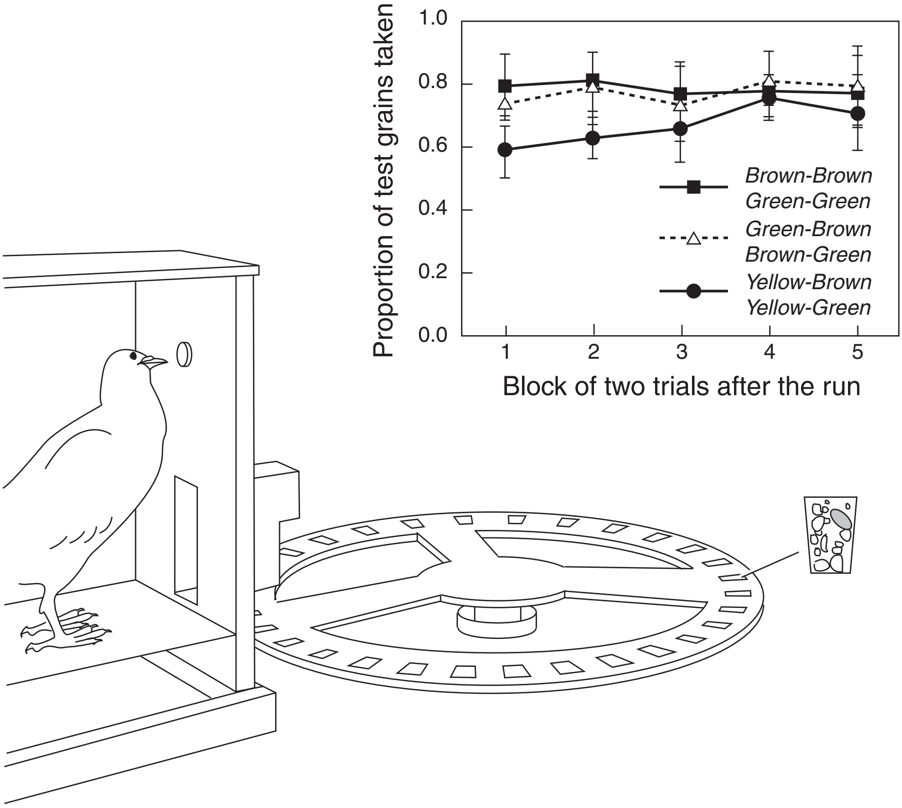


Figure 3.19. Search image effects in pigeons searching for cryptic brown or green or conspicuous yellow grains. Data from a test run of 10 grains after a run of the same or a different color, as indicated. Adapted from Reid and Shettleworth (1992) with permission.

single salient feature (color). The cryptic grains are difficult to detect because they resemble the distractors in color. Because the cryptic items were all grains of wheat, priming with grains dyed one color could enhance detection of other grains with the same shape, size, and texture. The effect on choice shows that the specific color was also primed to some extent. Such a priming effect occurs even if the priming grains are conspicuous, but it is detected only in a test with cryptic grains (Langley 1996). Thus, contrary to the fanciful depictions in Figure 3.16, the "search image" is a collection of independently primed features of the prey. This interpretation suggests that when, unlike the case in Reid's experiments, two cryptic items do not share features allowing them to be detected against their background, the search image/priming effect should be truly specific, with enhanced detection of one item accompanied by reduced detection of the other. Such an effect was observed in a study by Langley (1996) in which pigeons searched computer images of multicolored gravel for a bean or a grain of wheat. By manipulating features of the images, Langley also showed that the importance of color and shape differed for beans versus wheat (see also Plaisted and Mackintosh 1995).The type of background and the type of search task can also influence what features are attended to, as shown in an elegant study by Blough (2002) in which pigeons performed difficult detection and disambiguation tasks with a single set of striped disks. In summary, the "search image," that is, the representation or activation underlying sequential or associative priming, is rarely if ever an actual image of the item being searched for. Rather, what it consists of may vary from one situation and task to another depending on factors such as what distinguishes the item from the substrate and what features it shares with other concurrently available items.

The priming effects we have been discussing are by definition short-lived. Indeed, Bond (1983) suggested that sequential priming decays after a few seconds. But this raises a question about the interpretation of some findings reviewed in this section. For instance, consider that in Reid and Shettleworth's (1992) study two green grains were separated by twice as long on average in mixed green and brown trials as in green-only trials. When pigeons are detecting small black and white patterns against black and white checked backgrounds, a difference in presentation rate by itself can produce differences in discrimination accuracy (Plaisted, 1997). When items in runs were presented at the same rate as items of a single type were occurring in mixed trials, accuracy was no greater than in the matched mixed trials. Plaisted (1997) therefore proposed that search image effects reflect a short-lived priming of independent memory traces for recent items rather than priming of attention to particular item features. However, although this methodological feature should be to taken into account in studies of priming, so far there is no evidence that Plaisted's proposal accounts for results such as those discussed earlier in this section (Bond and Kamil 1999; Blough 2001; Blough 2006; Kamil and Bond 2006).

3.7.2 Search images and prey evolution

Attentional priming has implications for the evolution of species that are prey. For example cryptic prey of a single species should spread themselves out in the environment to reduce the chances of predators encountering them in runs. *Polymorphism,* that is, a tendency for different individuals of the same species to have markedly different colors or patterns, would have the same effect (Croze 1970; Bond 2007). But it is one thing to speculate on how predator psychology has selected for prey appearance and behavior, another thing to demonstrate that this could actually happen. Such a demonstration is provided by a series of studies with bluejays, using procedures similar to those of Pietrewicz and Kamil (1981) but with computer-generated "moths" (Figure 3.20) that "evolve" in response to predation (Kamil and Bond 2006). In the first experiment with this "virtual ecology" (Bond and Kamil 1998; Kamil and Bond 2001) the initial prey population consisted of three "species," digitized images of *Catocala* moths. They appeared on a background of random pixels that could vary from almost smooth grey on which the moths were very conspicuous to a mixture of patches similar to the patches on the moths. Bluejays that had been trained to detect the moths under very cryptic conditions then became the selective agents in the following way. Every day 240 moth images were used. In the first day of the experiment there were 80 of each species (Figure 3.20). At the end of each day, the moths detected by the jays were considered killed, and the remaining moths were allowed to reproduce (actually, here to clone themselves) to provide the population for the next day. In this way the least detectable moths became proportionately more numerous in the next virtual generation.

In three repetitions of this procedure with different initial conditions, the same moth (moth 1 in Figure 3.20)—evidently the most cryptic of the three—came to dominate. This was true even when it was in the minority to begin with, as in the

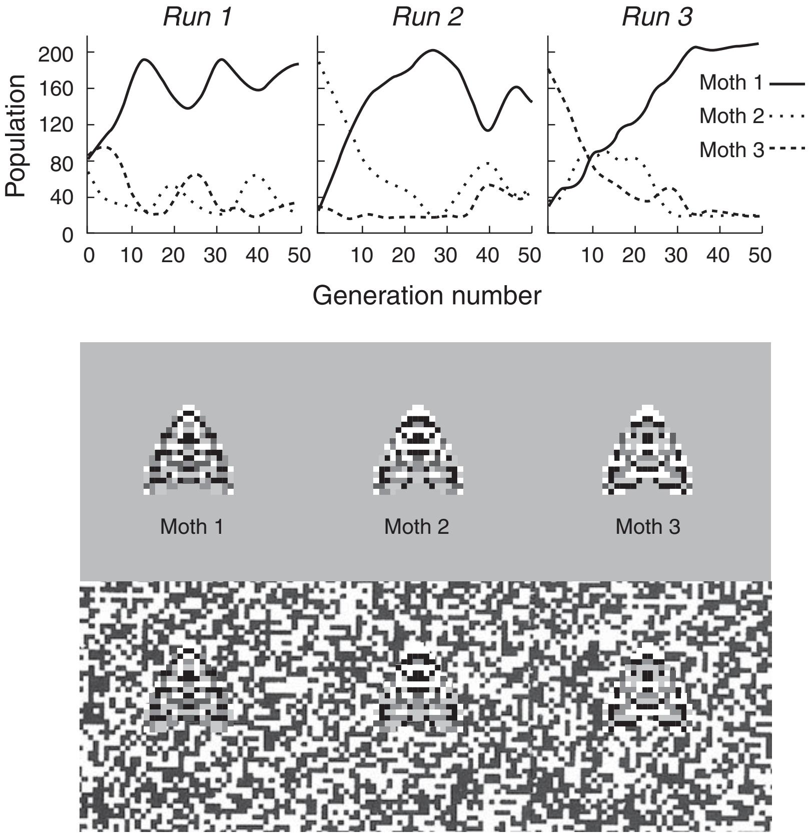


Figure 3.20. Lower panels: the three artificial moth species in Bond and Kamil's (1998) "virtual ecology" shown in both easy (gray background) and hard to discriminate conditions. Upper panel: changes in the virtual population over generations of predation by jays given different compositions of the initial population (Runs 1–3). After Bond and Kamil (1998) with permission.

second and third replications. The jays were showing the same kind of *frequency-dependent selection* evident in Bond's (1983) pigeons (Figure 3.17). A separate study (Bond and Kamil 1999) demonstrated that indeed jays show attentional priming effects with such digital moth displays. As the relatively conspicuous moths 2 and 3 were eliminated, individuals of moth 1 were found more often, priming detection. At the final abundances in each repetition, the intrinisically greater detectability of moths 2 and 3 was balanced by the primed detectability of moth 1.

The next step with this approach was to model evolution more realistically by modeling the genetics of wing patterns and letting the surviving virtual moths from a large and varied initial population "reproduce" via an algorithm that randomly recombined genes for different aspects of wing patterns (Bond and Kamil 2002; Bond and Kamil 2006). The populations that resulted from 100 generations of selection by jays were more cryptic and more diverse in appearance than control populations. Analysis of the sequences of events within sessions of the experiment showed that, just as would be expected, accuracy at detecting one of the more cryptic moths was better the more similar it was to the last moth detected. In summary, then, this approach shows that search image effects are still at work even in a dynamic situation with multiple prey types, and that—just has been commonly hypothesized—they can have an important impact on prey evolution.

The results of all these studies with "virtual ecology" imply that the learning and attentional mechanisms of predators can help to maintain polymorphisms in populations of a single species by leading to *frequency dependent selection,* that is, as a type of prey becomes more frequent it is proportionately more preyed on (Bond 2007). The different prey types, which may be morphs of a single type, do not have to differ in crypticity. If one type is rare for any reason, it should have a survival advantage. Thus Figure 3.17 illustrates frequency-dependent predation when the "prey" are different kinds of grains. In a nice demonstration in the wild, male guppies with different tail color patterns were removed from isolated natural pools in Trinidad, recombined into experimental populations in which one tail color pattern or another was comparatively rare, and reintroduced. Males chosen to have a color pattern that was uncommon in their group were most likely to survive until the pool was re sampled 2 to 3 weeks later (Olendorf et al. 2006).

3.7.3 Divided attention and vigilance

An animal that is foraging cannot wait until it is satiated to check for predators but should continuously divide attention between foraging and vigilance. The classic illustration of how hard it is for people to divide attention is the situation at a cocktail party: when many conversations are going on simultaneously, it is very difficult to follow more than one of them at a time. In tests of divided attention in the laboratory (see Luck and Vevera 2002), people are instructed to report on more than one source of information at once. In general, performance on a given task falls when attention must be shared between it and another task. The same is true in animals tested in common laboratory paradigms, most often short-term memory tasks (Chapter 7; Zentall 2005a). Just as in the tests of focused attention discussed up to now in this chapter, the detrimental effect of divided attention may diminish as practice leads to automatization (Schiffrin 1988), consistent with the idea that well-learned tasks demand fewer processing resources.

Birds that feed on the ground have been popular subjects for naturalistic studies of dividing visual attention between feeding and vigilance. Many such birds alternate short periods with their heads down, presumably attending to food-related cues, with short periods of head-up scanning, presumably attending to predator-related and/or social cues. For instance, members of a flock of starlings walking across a field probing the ground for leatherjackets raise their heads between pecks and scan the sky and bushes. The smaller the flock, the more time each individual spends scanning (Elgar 1989). More demanding foraging tasks leave less time for vigilance. For example, when blackbirds are foraging on cryptic baits they take longer between scans and spend a smaller proportion of the time scanning than when they are feeding on conspicuous baits (Lawrence 1984).

However, the assumption that head position defines the focus of attention is problematical. For one thing, as mentioned in Section 3.1, what an animal sees from different viewpoints depends on the structure of its visual system. Many birds have a wide field of view and an area of high density photoreceptors placed to detect things approaching from the side (Figure 3.3). As long as they have a clear field of view, with no low barriers, thick grass, or the like, birds may be able to spot a predator almost as well while feeding with head down as while scanning with head up (Lima and Bednekoff 1999; Fernandez-Juricic, Erichsen, and Kacelnik 2004). And in any case, most studies of divided attention in humans deal with a central filtering mechanism, not where the receptors are directed. Thus, although some animals do continually display brief bouts of vigilance while feeding, at the level of mechanism they may not be doing the same thing as person at a cocktail party who attends at one moment to Joe's voice and at the next to Pete's.

Fish have also been subjects in studies of the tradeoff between feeding and vigilance. Sticklebacks recently exposed to a model predator, a kingfisher, flying overhead, feed more slowly than fish not so exposed. It is not surprising that fear increases vigilance, that is, it redirects attention, just as any motivational state enhances the salience of relevant stimuli (Milinski and Heller 1978; Milinski 1984). Suppressing feeding when preparing to flee has a function in that flight responses direct blood flow and other physiological resources away from digestion and toward the muscles for escaping. Independently of such motivational conflicts, a high feeding rate may indicate that less attention is available for predators. This was nicely demonstrated in an experiment in which guppies feeding on water fleas (*Daphnia*) were exposed to predation by a cichlid fish (Figure 3.21, Godin and Smith 1988). The amount of attention devoted to foraging, as reflected in the speed of capturing prey, was manipulated by varying both the density of *Daphnia* and the guppies' hunger level. The faster the guppies were feeding (i.e., at shorter intercapture intervals in Figure 3.21), the more likely one was to be captured by the cichlid. Animals foraging in a group may also need to monitor social stimuli, experiencing a three-way conflict among feeding, watching for predators, and seeing what companions are doing. For instance, juvenile brown trout feeding with familiar companions fed faster and responded more quickly to a model heron than did trout with novel companions, who instead spent more time in aggressive interactions (Cresswell et al. 2003).

Dividing attention in all these naturalistic situations seems to have clear costs such as lower feeding rate or increased risk of being caught by a predator, but the most direct demonstration of such a cost is perhaps that by Dukas and Kamil (2000). Bluejays were trained to find cryptic items among distractors in a central area and two

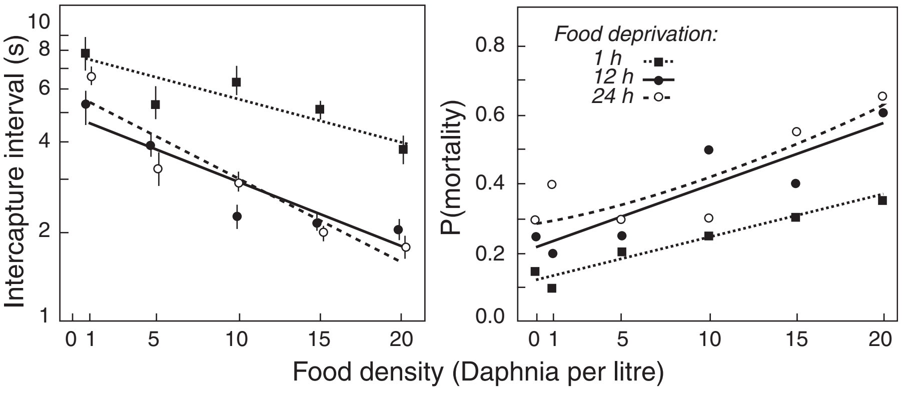


Figure 3.21. Effects of food density on guppies' feeding rate (the inverse of the interval between prey captures, left panel) and predation risk, the number of guppies caught by a predator. Redrawn from Godin and Smith (1988) with permission.

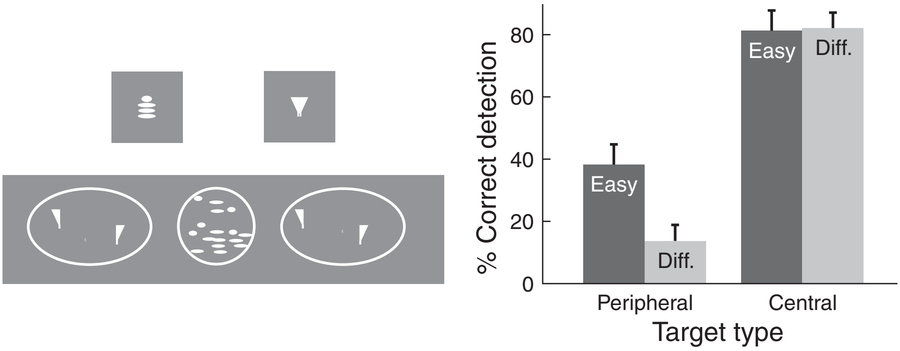


Figure 3.22. Procedure and results from Dukas and Kamil's (2000) demonstration of the cost of limited attention in bluejays. On the left, the two possible "prey items" are shown above a depiction of the video screen on a typical trial, with distracting elements present in the peripheral and central areas. Data, on the right, compare detection rate with prey in the central versus peripheral areas and when the task was relatively easy or difficult ("diff."). Adapted from Dukas and Kamil (2000) with permission.

peripheral areas on a video monitor (Figure 3.22). Birds pecked the center of the screen to cause the three prey-containing areas to appear for 500 milliseconds. They then had another 1000 milliseconds to peck the one area where a prey item had just appeared. Making the display brief and requiring the birds to peck the center of the screen ensured that they were always looking in the same place when the display appeared, much as people are required to look at a central fixation point in analogous tests. And by having competing foraging tasks Dukas and Kamil ensured that they were not measuring a change in vigilance associated with a motivational change, for example from hunger to fear. The jays were expected to devote most attention to the central part of the monitor because an item appeared there on 50% of the trials, whereas one appeared in each peripheral area on only 25% of trials. And indeed, as the central task was made more difficult by increasing the number of distractors, presumably thereby increasing its demands on attention, birds missed more of the peripheral prey (Figure 3.22).

The *confusion effect* may be another manifestation of divided attention in naturalistic situations. The confusion effect refers to the observation that many species of predators have more difficulty capturing prey when confronting a large school, swarm, or flock of similar individuals than when confronting one or a small group of individuals (Miller 1922; Krakauer 1995; Schradin 2000). The probability of an attack ending in prey capture once it has been initiated can decline dramatically with increases in the number of individuals in the group being attacked (Magurran 1990). The confusion effect has generally (cf. Krakauer 1995) been interpreted as caused by the predator dividing its attention among the prey rather than focusing on one until capturing it. The individual in a school of identical conspecifics is the limiting case of a cryptic prey item because it is identical to the "background" of surrounding individuals. On this view it is not surprising that odd individuals or stragglers in a group tend to be the ones captured. Just as in visual search (e.g., P. Blough 1979), the larger the group, the more detectable an odd individual seems to be (Milinski 1990). Notice that the predator confronted with a dense school of prey is assumed to be dividing attention among two or more spatial locations, perhaps because the motion it perceives at each one automatically attracts attention.

The evolutionary determinants of group living and group size are important topics in behavioral ecology (see Chapters 12 and 13). The material in this section suggests that the difficulty of effectively dividing attention confers at least two benefits of living in groups. One is that each individual in a group does not have to take so much attention away from foraging for vigilance because others can warn it of approaching predators. The other is that by being in a group of similar looking individuals the potential prey animal benefits from the ability of the swarm to confuse a predator. The confusion effect may account for several features of swarming or schooling species such as the fact that they tend not to show sexual dimorphism (i.e., males and females look the same), that they crowd together more when threatened, and that mixed species groups tend either to consist of species that look similar or to break up into same-species groups in the presence of a predator (Landeau and Terborgh 1986; Tegeder and Krause 1995).

3.8 Summary

Many universal principles of perception reflect the organization of the physical world (Shepard 1994). Paradoxically, some of the best support for such an adaptationist view of perception is diversity: general mechanisms have been tweaked by evolution in an adaptive way for each species. Animals differ dramatically in the sensory channels they use and in the patterns of sensitivity of those channels. Differences in sensory systems among species can be related to differences in their habitat and lifestyle. Nevertheless, all sensory systems that have been studied share some features, such as greater response to more intense stimuli, sensitivity to contrast, Weber's law, and a tendency to habituate.

Behavioral methods for discovering what animals perceive include testing natural behavior to the stimuli of interest and testing learned behavior using the methods of animal psychophysics. Signal detection theory is a general model of the discrimination of signals from background noise that applies to any situation where an animal has to make a difficult discrimination, and it has implications for the evolution of animal signals. In animal signaling systems, one animal provides a signal to which another animal, of the same or a different species, responds. Perception and the evolution of signals are therefore inextricably linked.

To understand how objects are perceived we have to go beyond sensitivities to individual stimulus modalities or features to ask how features are combined. One influential theory states that objects are perceived as the sum of individual primary features such as color and shape that co-occur at the same time and place. This feature integration theory is supported primarily by the performance of humans in visual search tasks, but some similar data have been reported from other species. To understand how behavior is controlled selectively by only some parts of the environment at any given time, it is necessary to understand attention. Characteristics of attention such as its susceptibility to priming have been studied in visual search tasks in humans and other animals. The apparent ability of foragers to form a search image, enabling them better to detect cryptic prey, may be explained by priming of attention to the features of the prey that best distinguish it from the background. Dividing attention between two or more tasks causes performance on each one to fall. The effects of divided attention can be seen in the tradeoff between foraging and vigilance and in the confusion effect, both of which create a selection pressure for animals to live in groups.

The story of research on search images is a good example of how hypotheses suggested by observations in the field were tested in the laboratory, using a whole range of approaches from the "naturalistic" to the "artificial," from tests in which animals search freely for familiar prey to those with controlled presentation of digital images. Some studies bridge the gap between tests of search image and those of visual search for abitrary targets like letters and shapes. And most recently, this research has come full circle in studies designed to to test hypotheses about how predators' attentional mechanisms drive the evolution of prey populations. Short-lived priming of feature detection is likely responsible for effects originally attributed to a search image for a prey item, but they do not mean that attentional priming is the only mechanism responsible for observations like Tinbergen's (1960). When animals first encounter novel prey items, they must learn to recognize them as prey and learn where to find them and how to capture and handle them, among other things. Each of these processes can be isolated and analyzed experimentally, as we will see in the next two chapters.

Further reading

This chapter has emphasized topics that connect perception with issues in behavioral ecology somewhat at the expense of the substantial work by comparative psychologists on more anthropocentric topics. More about such work can be found in the book edited by Wasserman and Zentall (2006b), the review by Spetch and Friedman (2006), and the online "cyberbook," *Avian Visual Cognition* (Cook 2001a). High-level introductions to basic topics in the psychological study of sensation and perception in humans, including attention, color vision, and signal detection theory, can be found in Volume 1 of *Stevens' Handbook of Experimental Psychology* (Yantis 2002).

Dusenbery's (1992) *Sensory Ecology* is an overview of the physical principles of information transmission, also covered in Bradbury and Vehrencamp's (1998) comprehensive text on the ecology and evolution of animal communication. The books by Maynard Smith and Harper (2003) and Searcy and Nowicki (2005) are both excellent briefer introductions to animal signaling, topics that we come back to in Chapter 14. Lythgoe's (1979) *The Ecology of Vision* is a classic, a rich source of information about adaptations in animal visual systems that has not been replaced. Kelber et al. (2003) is a comprehensive review of the mechanisms and distribution of animal color vision. A brief overview of methods in animal psychophysics is provided by Blough and Blough (1977). The two papers by Wiley (1994, 2006) are excellent introductions to signal detection theory and its implications for issues in animal communication.

4
Learning: Introduction and Pavlovian Conditioning

Like *attention, consciousness,* and other words from ordinary language used in psychology, *learning* is a term that everyone understands even though it eludes satisfactory technical definition (Section 4.2.1; Rescorla 2007). Functionally, learning allows animals to adjust their behavior to the local environment through individual experience. Animals need to know such things as what locally available food is good to eat, where and when to find it, which individuals to avoid and which to approach. This chapter introduces a basic framework for thinking about learning and then considers some ideas about the function and evolution of learning. The longest part of the chapter reviews data and theory about Pavlovian conditioning, perhaps the best-studied form of learning and one of the phylogenetically most widespread. Armed with this framework and some facts about conditioning, we will be in a position to analyze other forms of learning in future chapters. We will also be equipped to assess claims that some animals sometimes behave in ways that cannot be only the products of conditioning but rather require reasoning, a theory of mind, a qualitatively different kind of learning, or the like.

4.1 General processes and "constraints on learning"

As we have seen in Chapter 1, experimental studies of learning and other aspects of cognition in animals were stimulated by Darwin's (1871) claim that animal minds share properties with human minds. Early in their history, studies of learning came to focus on instrumental (operant) and later classical (Pavlovian) conditioning (Jenkins 1979; Boakes 1984), while other kinds of learning and cognitive processes were largely overlooked. The result was an approach referred to as general process learning theory (Seligman 1970), an attempt to account for all learning with the same set of principles. Although there were a few dissenters (Tolman 1949), general process learning theory had a heyday in the 1940s and 1950s and remains tremendously influential.

In the mid-1960s, however, psychologists discovered several puzzling phenomena that the supposedly general learning principles did not seem explain (Seligman 1970; Rozin and Kalat 1971; Shettleworth 1972). The key examples of these "constraints on learning" were conditioned taste aversion (Box 4.1), and autoshaping.

In autoshaping (Brown and Jenkins 1968), pigeons are placed in an operant chamber and a disk on the wall (the pecking key) is lit for a few seconds before food is presented. The pigeon does not have to peck the key, yet after a number of pairings between the keylight and food, pecking develops and persists. This finding seemed related to the Brelands' (Breland and Breland 1961) reports that animals being reinforced with food engaged in counterproductive species-specific food-related behaviors or "misbehaviors." For instance, a raccoon rewarded for depositing coins in a bank began to "wash" and rub the coins together in its paws rather than promptly getting its reward. Attention was also drawn to the difficulty of training rats to perform anything other than natural defensive behaviors when learning to avoid shock (Bolles 1970). To such observations of constraints on what animals could learn (or at least, do) in laboratory paradigms was added information about song learning, imprinting, and other "exceptional" examples of learning observed by ethologists.

Box 4.1 Flavor Aversion Learning

When rats and many other vertebrates sample a flavor and become ill later, they learn to avoid consuming that flavor. As first described by John Garcia and his colleagues in 1966, flavor aversion learning has two remarkable properties. First, it takes place even with delays of hours between sampling the flavor (the CS in this Pavlovian paradigm) and becoming ill (the US; Garcia, Ervin, and Koelling 1966). Second, in rats, learning with illness as a US is specific to flavors. Garcia and Koelling (1966) had rats drink from a tube of flavored solution and also exposed them to a noise and a light each time they licked ("bright noisy tasty water"). Some of the rats were made ill after drinking, whereas some were shocked through the feet as they drank. When tested with the light plus the noise or the flavor alone after conditioning, the poisoned rats avoided drinking the "tasty water" while the rats that had been shocked avoided drinking the "bright noisy water." Figure B4.1displays data from a later experiment with this basic design but with the mode of presentation of the various CSs and USs

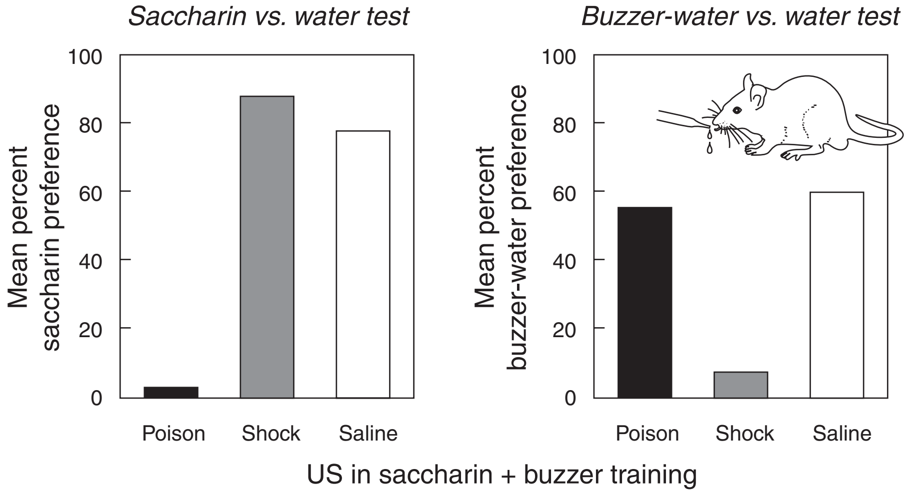


Figure B4.1. Test performance of three groups of rats that had experienced saccharin flavored water infused into their mouths while hearing the sound of a buzzer and had then been shocked, injected with lithium chloride to produce illness (poison US), or given a control saline injection. In the test rats chose between plain water and either saccharin (left panel) or water in a bottle that produced a buzzing sound when licked. Redrawn from Domjan and Wilson (1972) with permission.

better controlled than in the original (Domjan and Wilson 1972). These findings attracted tremendous attention when they were first reported because long-delay learning and CS-US specificity seemed to contradict then-current assumptions about the generality of the laws of learning. Some investigators rushed to test hypotheses that various uninteresting "general process" factors might have been responsible, while others were equally quick to claim far-reaching implications for them (Domjan and Galef 1983). The idea that learning may be especially fast with certain functionally appropriate combinations of events is now generally accepted (Section 4.4.4).

Conditioned taste aversion is a good example of how the details of conditioning in different systems can differ in an adaptive way: if the effects of ingesting something with a certain flavor can only be felt hours later, the learning mechanism for avoiding illness-producing foods should be capable of bridging this temporal gap. Strictly speaking, however, conclusions about adaptation require showing that animals with the hypothesized adaptation have greater fitness than animals lacking it or doing comparative studies. In the case of taste aversion, species that specialize on one or a few foods might have less need to learn flavor aversions than generalist species, that is, those which sample a variety of foods. Although a test of this hypothesis with two species of kangaroo rats (Daly, Rauschenberger, and Behrends 1982) provided only weak support for it, a test with four species of bats had clear positive results. Vampire bats, which consume only blood, showed no evidence of learning a flavor aversion, whereas three species with a varied diet of insects or fruit readily learned under the same conditions (Ratcliffe, Fenton, and Galef 2003).

Around 1970 several articles appeared on the theme that general process theory had overlooked the biological aspects of learning (Bolles 1970; Seligman 1970; Rozin and Kalat 1971; Garcia, McGowan, and Green 1972; Shettleworth 1972). They suggested that the newly discovered phenomena could be understood in terms of the idea that learning evolved for solving problems animals face in nature. However, despite proclamations that a revolution in the study of learning was on its way, the original candidates for "biological constraints" and "adaptive specializations" were gradually absorbed into a liberalized general theory of associative learning (Domjan 1983). At the same time, by not formulating a clear research program with testable predictions, proponents of the "biological constraints" approach failed to stimulate research into related phenomena that might have been better examples of adaptive specialization of learning (Domjan and Galef 1983). The term "constraints" in itself implies a general process that is constrained in particular species and situations. But it is more appropriate to think in terms of evolved predispositions or adaptive specializations than in terms of constraints (Section 2.5 and Hinde and Stevenson-Hinde 1973). Recent developments in the study of behavior and cognition reviewed in Section 1.5 have similarly absorbed "constraints on learning" into a more biologically oriented approach to psychology in general.

4.2 A framework for thinking about learning

4.2.1 What is learning?

Learning, or equivalently memory, is a change in state due to experience. Obviously, this definition includes too much. For instance, 24 hours without food changes a rat's state so it is more likely to eat when given food again, but this change in state is called hunger, not learning. Running 10 kilometers a day improves a person's endurance, but although a person may learn something from doing it, physical training is not normally called learning either. The changes in state referred to as learning seem to involve a change in cognitive state, not just behavioral potential, but this is helpful only if cognitive can be distinguished from other kinds of changes.

So why start with such a broad definition? In the past learning has often been defined too restrictively, in a way that automatically rules out consideration of diverse and novel forms of behavioral plasticity (Rescorla and Holland 1976; Rescorla 2007). For example, saying that learning is the result of reinforced practice equates learning with instrumental conditioning. Specifying that learning must last for at least 24 hours implies that a small effect of experience lasting, say, 20 hours is qualitatively different from one lasting two days. Saying that motivational changes such as increases in hunger can be reversed easily while developmental changes like learning cannot (Hogan 1994b) does not specify where to draw the line between "easy to reverse" and "hard to reverse." Defining learning as a neuronal change (Dukas 2009) rules out potential examples in plants or bacteria but switches the focus from behavior to a less readily observed level. Beginning without too many constraints allows us to consider the broadest possible range of experience-induced cognitive changes.

The changes in state commonly referred to as *learning* (or *memory,* Chapter 7) have the potential to be read out in behavior. But by itself a change in behavior with experience is not diagnostic of learning. To decide whether or not any sort of learning has occurred, it is always necessary to compare two groups of individuals. One has the experience of interest at an initial time, T1. The other, control, group does not have that experience. In effect, therefore, the control has a different experience, and thoughtfully defining that experience is essential to understanding the nature of learning. In any case, the two groups given different experiences at T1 must be compared *on a standard test* at some later time, T2 (Rescorla and Holland 1976; Rescorla 1988b; Rescorla 2007). This simple but important notion is diagrammed in Figure 4.1a. To make it concrete, consider a simple demonstration (Figure 4.1b). Suppose we want to know whether male canaries learn how to sing from other canaries. A first step would be to raise some male canaries in isolation and others in normal social groups. The rearing period, during which the birds are treated differently, is T1. We might well observe that males in social groups begin to sing more or in a different way than isolated males, but we would not know whether this difference in behavior at T1 reflects learning. For instance, maybe being with other birds in itself stimulates young males to sing more or in a different way. This is why the standard test at T2 is necessary. Here, this test might consist of placing each male with a female and recording his vocalizations. We might observe that the socially raised males sang more complex and varied songs than those raised in isolation. We could safely conclude that some learning had occurred, but we could not conclude that the *form* of the songs was learned. Maybe, for instance, the males raised in isolation are frightened of the females and behave differently from males that are familiar with females for that reason. Further comparisons would be necessary to isolate such factors. For instance, in many studies of song learning a possible role for differences in social experience is ruled out by raising all the birds in isolation and playing them tape-recorded songs.

4.2.2 Three dimensions of learning

Three basic questions can be asked about any learning phenomenon (Rescorla 2007): What are the conditions (or circumstances) that bring learning about? What is

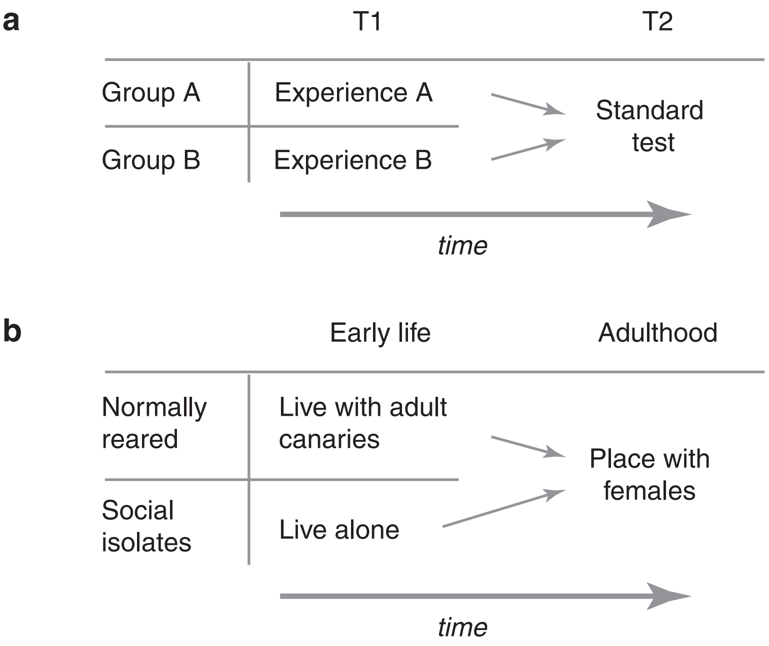


Figure 4.1. a. Essentials of any experiment designed to demonstrate learning. b. The abstract design illustrated by a test of the contribution of early experience to adult behavior in canaries.

learned? How does learning affect behavior? Of course one can ask other questions about learning, too. How widespread among species is it? What function does it serve? How did it evolve? How does it develop within the individual's lifetime? What neural and molecular processes underlie it? However, most experimental analyses of learning at the behavioral level have been directed toward understanding the conditions for learning, the contents of learning, or its effects on behavior.

Conditions for learning

The first step in understanding any instance of learning is to analyze the conditions that bring it about. What kind of experience is necessary for the behavioral change that we are interested in? Does the age, the sex, the species, or the past experience of the subject matter? In our example of song learning in canaries, studying the conditions for learning might involve exposing different groups of birds to various amounts and kinds of auditory input and doing so when they are at different ages. In general, when relevant experience is repeated more often, lasts longer, and/or is more intense, more learning occurs, as measured in some way like how many subjects show the behavioral change of interest, how much of it they show, or how long it lasts. Qualitative features of experience usually matter. For instance, while canaries may learn the song of another canary, they might show less evidence of learning if they have heard the song of a sparrow under similar conditions.

Which of the many possible conditions for learning to investigate is a decision based, if only implicitly, on assumptions about what kinds of events are likely to be important. For example, our experiments on bird song are unlikely to include tests of the effects of barometric pressure, but they are likely to include comparisons of the effects of songs from the bird's own vs. another species. Choice of what to look at is often based on the assumption that in general the function of learning is to allow an animal to fine-tune its behavior to the specific environmental conditions it encounters during its lifetime. If the male canary learns his song at all, he is likely to learn from canaries, not sparrows. However, experiences seemingly having little to do with the function of a behavior may play an important role in its development. For example, if ducklings do not hear their own vocalizations while they are still in the egg, they do not prefer calls from adults of their species after they hatch (Gottlieb 1978). A strictly functional approach can mislead investigators into overlooking such effects. Indeed, they are not usually classified as "learning" (Hogan 1994a), although the conditions underlying developmental changes may not differ from those underlying "learning."

Some conditions for learning reflect reliable patterns of events in the world. For instance, the more something has occurred in the past, the more likely it is to occur in the future. Thus behavior should be better adjusted to frequently recurring events than to rare ones. An event of great biological importance, like arrival of a fierce predator or a large meal, requires more or faster changes in behavior than a small and insignificant one, and learning is accordingly faster and more complete the larger the reinforcer. Such properties of learning seem so obvious and reasonable that it is easy to forget they are not necessary features of the way behavior or the nervous system changes with experience. They are reminders that evolution has selected for nervous systems that respond adaptively to experience.

Contents of learning

Questions about the contents of learning, that is, what is learned, are of two sorts. Easiest to answer are those at the level of data. For example, we might want to know what features of song our male canaries learned. We could try to find out by varying the notes and phases in the training songs and seeing if this variation is reflected in the subject canaries' singing. The harder questions about what is learned are the theoretical ones. What hypothetical internal cognitive structure accounts for the observed relationships between experience and behavioral change? A classic answer is that experience changes the strength of an association, an excitatory or inhibitory connection between stimuli and/or responses (Dickinson 2007). The contemporary cognitivist's answer (e.g., Gallistel 1990) is more likely to be that experience changes a more complex representation of some aspect of the world. As we see in Section 4.5.2, there is currently some debate about what is learned in conditioning. For other types of learning, the underlying representation is referred to as a cognitive map, a neuronal model, or a template, among other things. For instance, the now-classic model of song learning depicts the effects of experience with song as being stored in an auditory template against which the bird matches its own vocal output (see Box 13.2).

Effects of learning on behavior

If learning is thought of, as it is by radical behaviorists, as nothing more than change in behavior, questions about the contents of learning never arise. They arise only if observable behavioral changes are seen as the readout of underlying cognitive changes. That is, these questions assume a distinction between learning and *performance* based on that learning, between what the animal knows and what it does. For instance, a young male white-crowned sparrow is normally exposed to the songs of adults during his first summer, but he will not begin to sing himself until the next spring. The learned information is stored for months, until singing is stimulated by seasonal hormonal changes (Marler and Peters 1981). We can find out what the animal knows only by observing what it does (though techniques for imaging brain activity may be changing that). Nevertheless, the knowledge exists even when it is behaviorally silent. A theory of how learning translates into performance needs to specify what behavior will occur as a result of learning. For instance, in terms of the model of behavior discussed in Chapter 2, one might ask whether an experience changes a single motor pattern or a whole behavior system. A hallmark of change in a central cognitive representation is that it can be reflected in behavior in a flexible way. For instance, when marsh tits (*Parus palustris*) have stored food in sites in the laboratory, they show that they remember the locations of those sites in two different ways. When they are hungry and presumably searching for food, they return directly to the sites holding hoarded food. In contrast, when they are given more food to store, they go to new, empty, sites (Shettleworth and Krebs 1982). Thus rather than merely returning automatically to the sites with food, the birds seem to have a memory for the locations with food which they can act on in a flexible and functionally appropriate way.

4.3 When and how will learning evolve?

If the world were always the same, learning would be more costly than fixed behavior. In an entirely unpredictable world, there would be no point in learning anything. The predictable unpredictability favoring the evolution of learning exists when some environmental condition important for fitness changes across generations but remains the same within generations (Johnston 1982; Stephens 1991). But this description applies to most forms of phenotypic plasticity (Dukas 1998). For example, in the presence of chemicals from predators, tadpoles of some North American frog species develop longer tails and smaller bodies, making them better able to escape predators (see Miner et al. 2005). Caterpillars of the moth *Nemoria arizonaria* that hatch from eggs laid early in the season eat oak pollen and develop to resemble the oak catkins where they prefer to rest. Their kin hatched from eggs laid later in the season feed on oak leaves, and they resemble and rest on oak twigs (Greene 1989). What the caterpillar finds around it to eat when it hatches reliably predicts how best to be cryptic, and accordingly chemicals in the food induce these differences in morphology and behavior. Such *inducing effects* of the environment are useful when reliable sensory information about local conditions is available from early in the organism's development. Unlike some other forms of phenotypic plasticity, learning is usually (but not always; imprinting, in Chapter 5, may be an exception) potentially reversible, reflecting the fact that a given kind of information may change over time. For example, honeybees readily acquire a preference for the color of flowers that currently have the most nectar, but they learn a new color preference when new plants begin to flower (Dukas 1998).

Functionally, by learning animals acquire sensory information about local conditions that is useful in determining future behavior (Gallistel 2003). The kind of thing that needs to be learned must be the same in every generation, otherwise any given learning ability could not cope with between-generation variation. For instance, the location of food or a nest may vary from generation to generation, but there may always be some advantage in being able to learn and use the kinds of cues that predict such locations. The conditions that bring learning about should be reliable correlates of the state of the world that the animal needs to adjust to. This correlation is encoded in learning mechanisms so that experience brings about relevant, fitness-enhancing, changes in cognitive state and behavior. For instance it would be no good to a blue jay to associate the orange and black pattern of a Monarch butterfly with the emetic effects of ingesting it if this association caused the bird to attack Monarchs more avidly rather than rejecting them.

When learning is a matter of life or death, there is not time to try out all possible solutions to a problem while learning the best one. Animals, including human beings (Cosmides and Tooby 1992), must therefore be preprogrammed to take in only the most relevant information and use it in relevant ways. Lorenz (1965) called this tendency "the innate schoolmarm," emphasizing that learning is not possible without an underlying predisposition to learn. Gould (2002) similarly refers to "learning instincts." This idea leads to the prediction that multiple kinds of learning or memory systems or modules will evolve to deal with functionally incompatible requirements for processing different kinds of information (Sherry and Schacter 1987; Gallistel 1998; Shettleworth 2000; Gallistel 2003). For example, a nocturnal rodent or a desert ant leaving its underground nest to forage must rely on its own internal sense of the distance and direction it has moved from home in order to get back there when returning with food or escaping from a predator. The ability to acquire and act on this vector-like information, the capacity for path integration (Chapter 8), reflects a distinct cognitive module. For conditioning, by contrast, what matters is the relationship between events in time, as when a bee learns that arrival at certain flowers is followed by access to nectar or a jay learns that eating Monarch butterflies is followed by vomiting. Conditioning can of course affect an animal's movement through space, as when the bee approaches a rewarding flower, but unlike the vector information encoded for path integration the information necessary for learning is not inherently spatial.

Although people tend to think of learning as an unalloyed good, behavior dependent on learning does have a cost because almost by definition behavior will be less than optimal while the animal is acquiring the information it needs (T. D. Johnston 1982; Dukas 1998, 2009). For instance, many songbirds experience very high mortality during their first summer, partly because they are learning to forage efficiently on locally available prey. This is illustrated in Figure 4.2 in dramatic age differences in the time free-ranging yellow-eyed juncos (*Junco phaeonotus*) took to consume a mealworm provided by the experimenter. Recently independent juveniles spent most of the daylight hours foraging, yet 3.85% of them died every day (Sullivan 1988). Similarly, young European shags (*Phalacrocorax aristotelis*) may die in winter if they cannot forage fast enough to get sufficient food during the limited hours of daylight (Daunt et al. 2007). The costs of learning may therefore affect multiple aspects of life history in species that must learn about essential resources (T. D. Johnston 1982; Dukas 1998, 2009). For instance, the more that young animals need to learn before they can feed themselves, the longer they will remain dependent on parental feeding and the longer they will have to delay reproduction. Adults should not produce more young than they can feed to the age of independence, or their reproductive effort will be wasted. Thus long-lived animals with complex foraging skills, like chimpanzees and albatrosses, tend to have small families and long periods of association between parent and young (T. D. Johnston 1982).

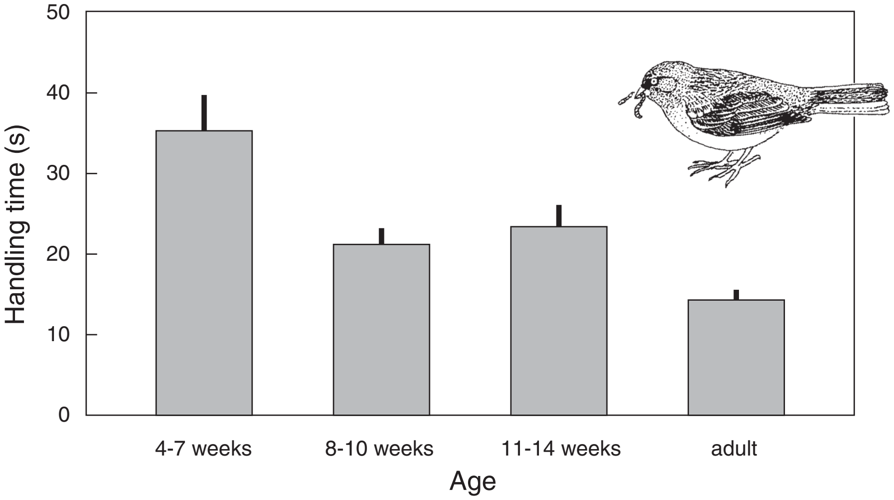


Figure 4.2. Development of foraging efficiency in yellow-eyed juncos, as indicated by reductions in the time taken to ingest a mealworm. Data from Sullivan (1988).

Of course, animals with short life spans such as bees learn too (Dukas 1998; Giurfa 2007). If resources are somewhat patchy in time and space, learning is favored (Krakauer and Rodriguez-Girones 1995), and this may be why bees have evolved such good learning abilities.

Evidence like that from Sullivan's (1988) study of the juncos is consistent with the assumption that learning evolved because it contributes to fitness. The ability to learn is so widespread among species that this assumption seems hardly to demand questioning. It has been tested, however, in a handful of experiments (Hollis et al. 1997; Domjan, Blesbois, and Williams 1998; Dukas and Bernays 2000; Dukas and Duan 2000; Domjan 2005). The logic was to deprive animals of the opportunity to learn about some resource by manipulating their environment and comparing their fitness (or some variable correlated with fitness) to that of animals experiencing the same cues and resources but in a predictive relationship. For example Dukas and Bernays (2000) compared growth rates of grasshoppers in two environments offering two kinds of food. For one group, the more nutritious food always had the same flavor and was on the same side of the cage with the same visual cue nearby. For the other group, the relationship of these cues to the two foods changed with every feeding. Thus these grasshoppers were deprived of the opportunity for learning that would allow them to find the better food efficiently, although after a few days they were able to reject the poorer food and switch once they began to eat it. Nevertheless, the grasshoppers deprived of the opportunity to learn grew more slowly than those provided with learnable cues, and because size is correlated with number of eggs laid, it seems likely that such inability to learn would have decreased their fitness. More direct measures of fitness have been used in some studies of the function of Pavlovian conditioning discussed in Section 4.7.3. Complementary to such studies are demonstrations (e.g., Mery and Kawecki 2002) that selection for learning ability does indeed result in lines better able to learn the kind of task that is the basis for selection. However, as when comparing learning across species (Chapter 3), careful controls are necessary before concluding that learning ability per se is being selected in such studies rather than sensory or motivational factors that improve performance.

4.4 Pavlovian conditioning: Conditions for learning

4.4.1 Background

In the prototypical example of Pavlovian conditioning, a dog stands on a platform with a fistula extending from its cheek, allowing its saliva to be measured drop by drop (Figure 4.3 top). A bell sounds, and shortly afterward the dog gets a morsel of food. The food itself evokes copious salivation, but after several pairings the dog begins to salivate when it hears the bell. The dog has undoubtedly learned something, but what has it learned, and what are the essential features of the experience that brings this learning about?

Historically, the ability of the bell to evoke salivation (a *conditioned response* or *CR*) was attributed to the transfer of control of a reflex (the *unconditioned response* or *UR* of salivation) from the innate eliciting stimulus of food (the *unconditioned stimulus* or *US*) to the initially neutral stimulus of the bell (the *conditioned stimulus* or *CS*). Now, however, learning theorists would be more likely to say that the dog has learned that the bell predicts food (Rescorla 1988a). Its salivation is merely conveniently measured evidence of that knowledge. If the dog were free to move about it might instead approach the feeder or beg and wag its tail at the sound of the bell (Jenkins et al. 1978). Indeed, in most of the currently popular experimental arrangements such as autoshaping (Figure 4.3 bottom), conditioning is measured by changes in behavior of the whole animal. On either interpretation, however, Pavlovian conditioning is seen as a case of *associative learning,* the formation of some sort of mental connection between representations of two stimuli. This statement conflates two meanings of *associative learning*. On a descriptive or operational level the term refers to learning resulting from the procedures involving contingencies among events specified in this upcoming section, that is, it is based on the conditions for learning. On a theoretical level, that dealing with the hypothetical contents of learning, associations are traditionally seen as excitatory or inhibitory links between event representations which do not themselves represent the nature of the link. Thus an encounter with a previously learned CS, A, simply arouses or suppresses a memory of its associate, B. More recently developed views are discussed in Section 4.5. These include suggestions that an association is equivalent to a proposition such as "A causes B" (see De Houwer 2009) and that the performance based on associative learning procedures does not reflect associative links at all.

The rest of this chapter is a bare-bones review of the properties of conditioning, as exemplified by Pavlovian (or classical) conditioning. It is organized in terms of the three aspects of learning introduced in Section 4.2: the conditions for learning, the contents of learning, and the effects of learning on behavior. There are at least four reasons for discussing Pavlovian conditioning before any other examples of learning. First, we know more about it than about any other form of learning. The analysis of Pavlovian conditioning thus illustrates how to answer the three central questions about learning in great depth and thereby provides a model for how other learning phenomena can be studied. Second, although Pavlovian conditioning has been thought of as mere "spit and twitches," some examples of conditioning turn out to have complex and interesting cognitive content (Rescorla 1988a). Thus it belongs in

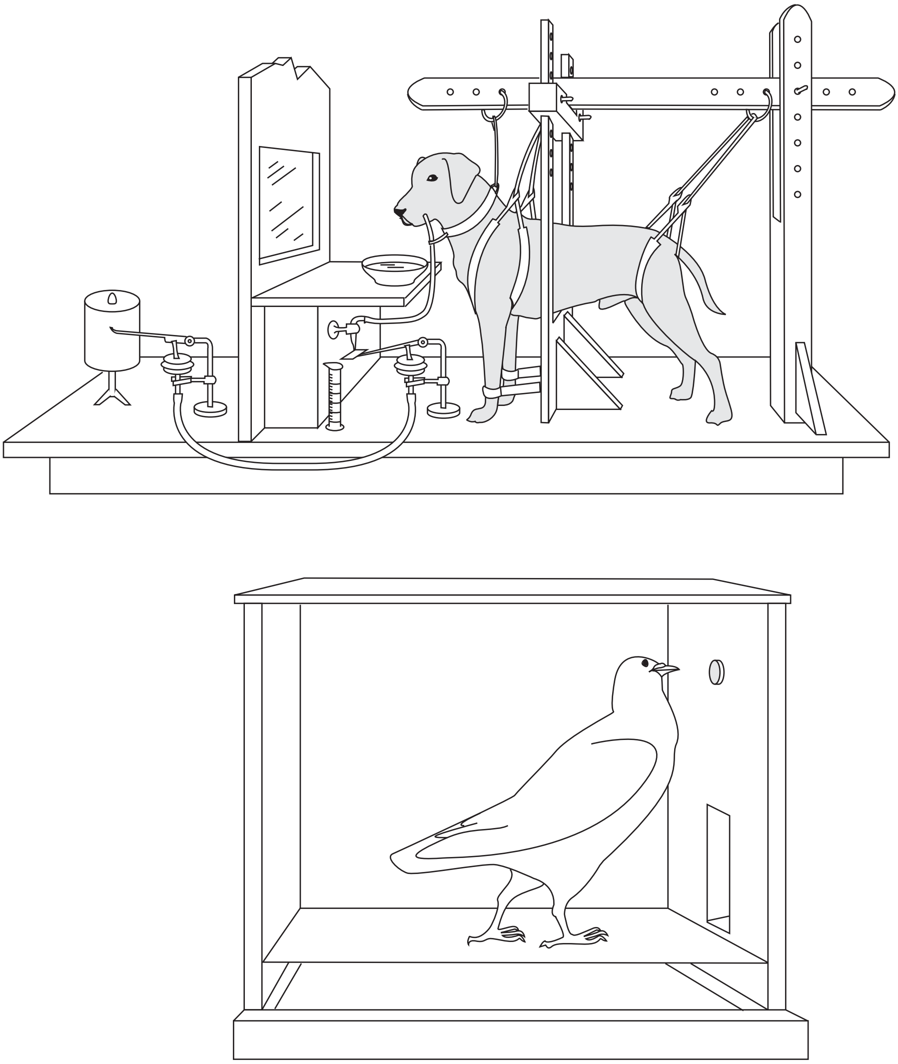


Figure 4.3. Two arrangements for studying Pavlovian conditioning. Upper panel, salivary conditioning in a dog, after Yerkes and Morgulis (1909). Lower panel, autoshaping in a pigeon, after Colwill (1996) with permission. In autoshaping, lighting of the pecking key (the disk on the wall) precedes delivery of food in the opening below it. The pigeon begins to peck the key even though food is given regardless of whether it pecks or not.

any account of animal cognition. Third, discussions of candidates for other forms of learning are usually organized around the question, “How is this different from conditioning?” To answer this question, we need to be familiar with the properties of conditioning. In the context of this book, it is especially important to appreciate the subtlety and complexity of what apparently simple animals can learn from apparently simple experiences. Finally, the basic phenomena of conditioning are phylogenetically very widespread, perhaps more so than any learning phenomena other than habituation (Papini 2008). Pavlovian conditioning allows animals to adjust their foraging, predator avoidance, social behavior, and many other aspects of existence to their individual circumstances. Moreover, the conditions for acquiring Pavlovian conditioning are formally largely the same as those for acquiring instrumental (or operant) conditioning, that is, learning the relationship between behavior and its outcome as opposed to learning the relationship between stimuli. The contents of instrumental learning and the effects on behavior of instrumental procedures may be different, however, as discussed in Chapter 11 in the context of other issues surrounding learning about the consequences of behavior.

A useful characterization of conditioning is that it is the process by which animals learn about predictive relationships between events and behave appropriately as a result (Dickinson 1980; Mackintosh 1983; Rescorla 1988b; Macphail 1996). This functional description makes very good sense of the conditions necessary for classical and instrumental conditioning. It also reflects the philosophical basis of the study of conditioning in associationism, which suggests that effects should be associated with their causes (Hall 1994; Young 1995). Associations have traditionally been thought of as the building blocks of all cognition, but seeing them as resulting from a distinct class of relationships makes associative learning just as adaptively specialized as, for example, learning about spatial or temporal relationships (Gallistel 2003).

The late 1960s and early 1970s saw a huge increase in research on conditioning, made possible by the development of arrangements for studying it that were more practical than the traditional salivary conditioning. For over 25 years this research was guided by the tremendously productive yet simple theory (Rescorla and Wagner 1972) discussed in the next section, which conceptualizes learning as changes in associative strength (R. Miller, Barnet, and Grahame 1995; Siegel and Allan 1996). More recent years have seen the formulation of several alternatives, each of which addresses particular shortcomings of Rescorla and Wagner's model, but all of which—perhaps inevitably–assume implicitly that what is learned is some sort of connection (Pearce and Bouton 2001; R. Miller and Escobar 2002; R. Miller 2006). Because there is as yet no generally accepted new model, this chapter follows other contemporary accounts in presenting the basic facts of conditioning and their interpretation within the context of the Rescorla-Wagner model, while pointing to some of its difficulties and how they are addressed by alternatives.

Nearly all of this section is based on data from vertebrates, mostly rats and pigeons. Invertebrates also show the basic phenomena of conditioning (Dukas 2008; Papini 2008). Indeed, an important body of research deals with the neural basis of learning in the simple nervous systems of species like the sea slug *Aplysia* (Krasne 2002). Fruitflies and nematode worms, along with mice, are now popular subjects for investigations of genetic and molecular mechanisms of learning (Matzel 2002). However, with the notable exception of honeybees (Bitterman 2000; Giurfa 2007; Papini 2008) species other than rats and pigeons have rarely been tested for all the phenomena central to theory development. Moreover, generally even rats and pigeons have been studied in only limited kinds of conditioning arrangements, such as autoshaping in the case of pigeons. A relatively recent development in conditioning research is the inclusion of comparable experiments on both rats and pigeons (e.g., Rescorla 2005)—or in some cases rats and humans (e.g., Arcediano, Escobar, and Miller 2005)—within a single article. Because different forms of conditioning are subserved by different neural circuits even within mammals (Box 4.2), one might wonder about the generality of all the aspects of conditioning described in upcoming pages. Indeed, some of the most revealing and provocative findings about the determinants and function of conditioned responding discussed in Section 4.7 come from research with unconventional conditioning arrangements (e.g., rats chasing ball bearings), behavior systems (e.g., sex and aggression), or species (e.g., Japanese quail, blue gourami fish). Basic mechanisms of conditioning remain powerful candidate explanations for any example of naturalistic learning in any species (e.g., Darst 2006), but given the considerable evidence (see R. Miller and Escobar 2002) that parameters such as choice of CS or amount of training influence details of the outcomes, it would not be surprising if species membership also determines the optimal parameter values, or indeed whether some phenomena occur at all. For example, as discussed in Chapter 11, the extent to which instrumental behavior reflects a representation of reward value rather than “mindless” habitual responding varies predictably within rats with amount of training, but it also varies across species, with fish always behaving habitually (Papini 2002).

Box 4.2 Conditioning, Genes, and the Brain: Commonalities and Contrasts

Although the basic phenomena of conditioning may be universal, their underlying neural and molecular mechanisms can differ across and even within species. For example, two of the best studied brain circuits involved in learning in mammals are those for fear and eyeblink conditioning (Fanselow and Poulos 2005). These are located in the amygdala and cerebellum, respectively. In each case, the essential neural circuit is specialized for detecting the coincidence of relevant CSs and USs within a specific time frame; repeated coincidence engages mechanisms for neural plasticity at the cellular (synaptic) level, but the genes and neurotransmitters or other cellular mechanisms may differ. Figure B4.2 is adapted from the extended discussion of these issues by Papini (2008) to show how learning mechanisms can be the same at one level and differ at others. Across species too, learning phenomena that are the same at the level of behavior can differ dramatically at other levels. Honeybees don’t have a cerebellum, an amygdala, or a hippocampus, but they still have a structure, the mushroom body, which integrates multisensory information (see Papini 2008). Bees show not only most basic phenomena of conditioning, but sophisticated spatial memory besides (Chapter 8).

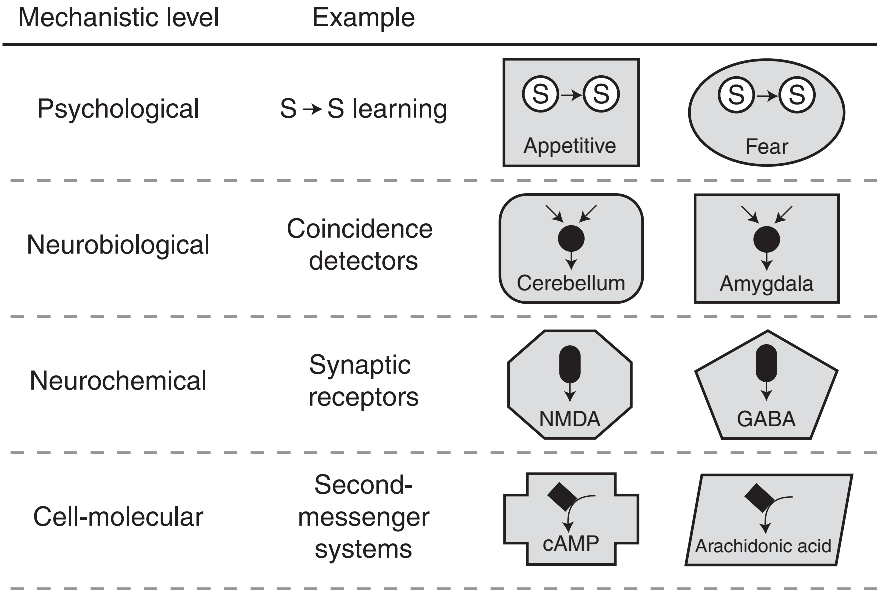


Figure B4.2. The different levels at which learning mechanisms may be compared within or across species. In this example, appetitive and fear conditioning are the same at the psychological level but access coincidence detection in different brain structures, where different neurochemical and molecular mechanisms are involved. Redrawn from Papini (2008) with permission.

The existence of multiple levels for analyzing mechanisms of learning and memory has important implications for thinking about the organization and evolution of learning and of cognition in general. Traditionally when psychologists refer to learning mechanisms they mean purely hypothetical underlying processes, as when competition for associative strength is said to be a mechanism for blocking and overshadowing. This is the principal level for discussing cognitive processes throughout this book. It is the basis for discussing, for example, whether aspects of memory or social behavior are functionally similar across species. However, similarity at the behavioral level does not necessarily represent strict homology in the sense of descent from common ancestors (see Chapter 2). Demonstrating homology requires the same mechanisms be shared right the way down to genes, and this is most likely in close relatives. Similarities of conditioning phenomena at the behavioral level in species that are not close relatives are often homoplasies (or analogies; see Chapter 2), possibly convergently evolved or evolved in parallel in different lineages. All the evidence now available on genetic and neural mechanisms of conditioning suggests that although conditioning can be treated as largely unitary at the behavioral level, the detailed neurobiological and molecular mechanisms for it may have evolved multiple times, perhaps reflecting the widespread functional importance of being able to learn that one event predicts another and at the same time the widespread availability of mechanisms for neural plasticity.

4.4.2 Contingency and surprise

To be sure that one is studying behavior reflecting the animal's experience of a CS predicting a US it is necessary to be able to discriminate this behavior from similar behavior brought about for other reasons. In the terminology of Section 4.2, animals that have experienced a predictive relationship between CS and US at T1 must behave differently at T2 from control animals that experienced some other relationship between CS and US. The best way to do this is to expose the control group to random occurrences of the CS and US. The behavior of these latter, random control, animals will reflect any effects of exposure to CS and US individually in the experimental context (Rescorla 1967). The effects of both positive contingency (CS predicts US) and negative contingency (CS predicts absence of US) can be assessed against this baseline (Figure 4.4).

The importance of the random control group was not always appreciated. Traditionally, temporal contiguity, or pairing, between two events was thought to be the necessary and sufficient condition for conditioning. The most popular control conditions eliminated contiguity by presenting only the CS or only the US or by presenting them systematically separated in time. But this experience has effects of its own. For instance, it can teach the animal that the US never follows the CS, thereby establishing the CS as a *conditioned inhibitor*. An alternative approach often used with invertebrates to establish that they can learn at all is differential conditioning with two CSs. When a US is paired with one CS and concurrently not paired with another, the animal should come to respond differently to the two CSs. However, as a test of CS-US associations, this design is subject to a subtle confounding from possible differential habituation, since habituation may be selectively prevented to a CS that is always quickly followed by a US (Colwill 1996). Colwill (1996) argues that the most conclusive tests of associative learning make use of the fact that, as reviewed in Section 4.5.1, a genuine CR reflects the quality and value of its US.

Even the relatively simple stimuli used in most laboratory experiments on conditioning have many features. For instance, a tone comes from a particular location

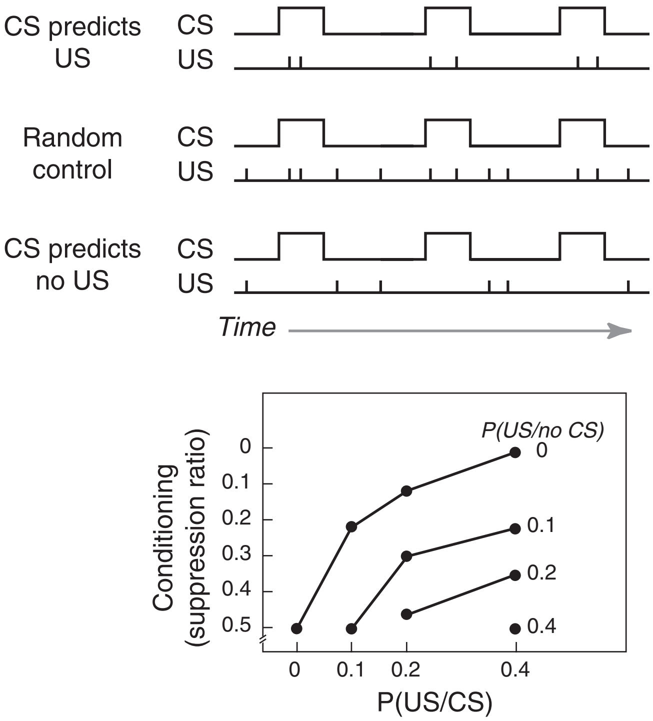


Figure 4.4. Effects of contingency on conditioning. In this example, illustrating the methods and results of Rescorla (1967), shock USs occurred with a constant probability per unit of time in the random control condition. Positive and negative contingencies were created by removing the USs between or during CSs, respectively. The effects of CS and US rates on fear conditioning are plotted as a function of the probability of shock during the CS, with a separate function for each probability of shock when no CS was present. Rats were bar-pressing for food and fear conditioning was indexed as the ratio between bar pressing rate during the CS and ongoing response rate. Zero suppression indicates maximal conditioning; 0.5 is minimal suppression. Redrawn from Rescorla (1988a).

and has a particular loudness and duration. A visual stimulus has brightness, size, shape, and perhaps other features. Are stimuli encoded as a unit or as a sum of features? And what about features that are added after initial learning? It turns out that if an animal has learned, say, that a light predicts food, and a new stimulus, say a tone, now accompanies the light so that the compound light + tone predicts food, learning about the tone, the new element, is reduced or absent (Kamin 1969). Like the contingency effects illustrated in Figure 4.4, this *blocking* effect means the CS must convey new information about the US in order for learning to occur. Mere temporal contiguity between CS and US is not enough. In the case of blocking, if the added CS does convey new information about the occurrence of the US, for example, when the US is now larger or smaller than it was when predicted by the first CS, animals do learn (Mackintosh 1978). Such *unblocking* shows that blocking is not merely due to a failure of attention to the added element. It suggests that animals associate two events only when the second one, the US, is somehow surprising or unexpected.

The notion that surprisingness or prediction error (Dickinson 2007) is essential for conditioning is captured formally in the influential Rescorla-Wagner model (Rescorla and Wagner 1972) referred to earlier. It generates the properties of conditioning

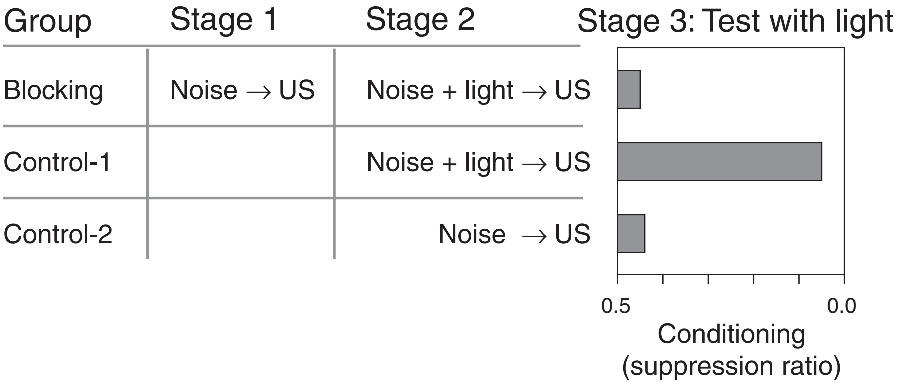


Figure 4.5. Design and results of Kamin's (1969) original demonstration of blocking of fear conditioning in rats. As in Figure 4.4, conditioning was measured by suppression of bar pressing: suppression ratios closer to zero correspond to greater conditioned fear.

reviewed so far and many others besides. A few of its assumptions are worth noting. One is that performance, that is, whatever behavioral index of learning is being measured, is monotonically related to the amount of underlying learning, or *associative strength*. Thus the model makes predictions about the relative level of conditioned responding in two or more conditions within a particular experiment, not absolute strengths of CRs. It also assumes that multifeatured events are treated as the sum of parts, rather than—as in one alternative model (Pearce 1994a)—a unique configuration. Thus the total associative strength, V, of a compound CS is the sum of strengths of its elements. The importance of surprise or prediction error is embodied in the assumption that the amount of associative strength a given CS accrues on a trial with a given US (ΔV) is proportional to the difference between the maximum associative strength that the US can support (the asymptote, λ) and the current associative strength of all CSs currently present (ΣV). The current associative strength of all CSs present corresponds to the degree to which the animal expects the US in the presence of those CSs. Learning is based on the discrepancy between what the animal needs to learn (λ) and what it already knows (see Figure 4.6). The parameters α and β in the equation are

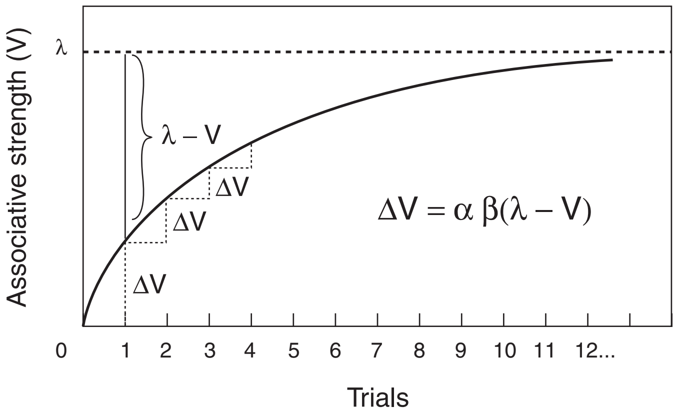


Figure 4.6. How the Rescorla-Wagner model generates a negatively accelerated learning curve.

constants related to the particular CS and US to reflect the fact that performance changes faster with salient or strong stimuli than with inconspicuous or weak ones.

The Rescorla-Wagner model readily accounts for blocking. When a novel stimulus, B, is added to an already-conditioned stimulus, A, the total associative strength of the compound is close to the maximum thanks to element A, so there is little left for B. The model also accounts for the effects of contingency as due to contiguity between CS and US by assuming that an explicit CS is actually a compound of CS and experimental context, that is, such things as the room where the experiment is carried out, the presence of the experimenter, and so on. When the predictive value of the CS is degraded by extra USs, as in Figure 4.4, the context becomes associated with the extra USs and leaves less room for conditioning to the CS. On this view, an animal exposed to random occurrences of CS and US is not an animal that has learned nothing; it may have associated the US with the environment or learned that the CS and US are unrelated.

The Rescorla-Wagner model also accounts for a second important form of competition between cues to the same outcome that was first described by Pavlov (1927), namely *overshadowing*. Because the gain in associative strength by each element of a compound is determined by the total associative strength of all stimuli present at the time, during training with a compound less is learned about either element than if it were trained alone. For example, a rat trained to expect shock after a light and a noise come on together will show less conditioned responding to the light alone than will rats trained for the same number of trials with light alone. The same goes for the tone, provided tone and light are of similar salience (α in the equations). Otherwise, the more salient element will do most of the overshadowing. It can be seen from the Rescorla-Wagner equations that overshadowing should occur only after the first trial of compound training. This prediction is not always fulfilled (Pearce and Bouton 2001).

Sometimes, too, the opposite of overshadowing is found, namely *potentiation*. That is, *more* is learned about a given cue when it is trained with a second cue than when it is trained alone. For example, conditioning to an odor is improved by training it in compound with a flavor rather than alone (Domjan 1983). This makes functional sense in that flavor can be seen as identifying the odors as a property of food and therefore worth learning about (Galef and Osborne 1978). When it was first discovered in taste aversion learning, potentiation was interpreted as a specific adaptation for learning about the properties of foods. However, potentiation occurs with other stimuli and in other conditioning situations (Domjan 1983; Graham et al. 2006). Some instances of potentiation are attributable to associations between elements of a compound CS (within-event learning, see Chapter 5). Thus, for example, rather than being directly associated with poison when they accompany a flavor, odors could be associated directly with the flavor and rejected because the flavor is aversive. Such effects suggest that the original claims that potentiation is a special kind of learning, a violation of the Rescorla-Wagner model, may not have been justified. However, the determinants of potentiation may be different in different situations (Graham et al. 2006), leaving open the possibility that it sometimes results from special mechanisms whereby one element of a compound enhances learning to another, perhaps by enhancing attention to it (LoLordo and Droungas 1989).

4.4.3 Associating CSs

In the most familiar examples of conditioning, the US is food, a painful stimulus, or some other event with preexperimental significance for the animal. Then learning is easy to measure because the animal usually behaves as if expecting the US when the CS occurs. Animals run about, salivate, peck, or gnaw in the presence of signals associated with food; they become immobile ("freeze"), squeak, or try to escape in the presence of danger signals. But preexisting biological significance is not essential for conditioning. In *sensory preconditioning,* two relatively neutral stimuli are presented with the same kinds of arrangements as in conditioning with food, shock, and the like. After such experience, the animal's knowledge about the events' relationship can be revealed by making one of the events behaviorally significant and observing behavior toward the other. For instance, if the animal first learns "tone is followed by light" and then "light is followed by food" it behaves as if making the inference, "tone is followed by food."

Second order conditioning is similar to sensory preconditioning in that initially neutral stimuli are used, but here one of them is given biological significance beforehand. That is, the animal first learns "light causes food" and then "tone causes light." When tested appropriately it behaves as if inferring that "tone causes food." Figure 4.7 depicts the experimental arrangements in these two paradigms. Some arrangements for studying conditioning in humans resemble those for sensory preconditioning in that the stimuli being learned about have little or no preexisting biological significance for the subject. This insight may be the key to understanding why some phenomena seen in first-order conditioning with animals fail to appear in humans (Denniston, Miller, and Matute 1996).

4.4.4 "Belongingness"

In the Rescorla-Wagner model the salience of the CS and US determine the speed of learning, through the parameters α and β, respectively. These values are fixed in the original model, though variants of it suggest experience can decrease (Pearce and Hall 1980) or increase (Mackintosh 1978) CS salience (for discussion of these models see Pearce and Bouton 2001). Contrary to any of these models, it may also matter how particular events are paired up. The best-known example is poison-avoidance learning (Box 4.1). In general, if associative learning is a mechanism for learning true causal relations, then if one event is a priori likely to cause another, it should take less evidence to convince the animal of its causal relationship than if it is a priori an unlikely cause. As this notion suggests, the importance of what has been called belongingness (Thorndike 1911/1970), preparedness (Seligman 1970), relevance (Dickinson 1980), or intrinsic relations between events (Rescorla and Holland 1976) has been demonstrated in a number of situations other than conditioned taste aversion (Domjan 1983). Far from being the evidence for special laws of learning it was once supposed to be, relevance or belongingness of stimuli is now recognized as a general principle of conditioning (R. Miller and Escobar 2002).

	Stage 1	Stage 2	Test
Sensory Preconditioning	A → B	B → US	A
Second Order Conditioning	B → US	A → B	A

Figure 4.7. Procedures for sensory preconditioning and second order conditioning.

Belongingness also plays a role in instrumental conditioning. For instance, pigeons more readily use visual than auditory stimuli as signals for food, but sounds are better than lights as danger signals. In both food-getting and shock-avoidance with pigeons, the "relevant" stimulus has a privileged status in that it cannot be blocked (LoLordo, Jacobs, and Foree 1982). Pigeons trained to press a treadle for grain in the presence of a tone still learned about an added light, whereas prior learning about the light did block the tone. Related effects are discussed in Section 4.7.4. Monkeys selectively develop fear to things like snakes that might be important to fear in the wild. A much-discussed suggestion (Davey 1995; Öhman and Mineka 2001, 2003) is that human phobias are underlain by an evolved predisposition to fear objects that were dangerous to our ancestors. For instance, people appear more likely to develop phobias toward things like snakes, spiders, mushrooms, or high places than flowers, electric outlets, soft beds, or fast cars. The propensity to develop fear to things that were dangerous in the evolutionary past is reflected in faster acquisition with snakes and the like as CSs in the laboratory, where it is specific to tasks with an aversive US (see Chapter 13 and Ohman and Mineka 2003).

Belongingness could reflect a preexisting connection that gives a head start to learning (LoLordo 1979; Davey 1995). Alternatively, experience of a given US may direct attention to certain kinds of stimuli. For instance, a rat that has recently been sick may subsequently pay particular attention to flavors. This possibility has been ruled out in the case of flavor aversions by exposing all animals to both USs of interest or by giving only a single training trial. However, it might be that illness specifically retrieves a memory of recently experienced flavors, making them available for association as in Wagner's model of learning discussed in Chapter 5. This mechanism would allow long delay learning in one trial. The possibility that prior learning plays a role can be addressed by using very young animals or animals with controlled past history. Finally, apparent belongingness may not represent different degrees of learning but differential readiness to exhibit that learning in performance. Evidence of learning might be seen especially readily, for example, if the response evoked by expectation of the US is similar to the response which the CS tends to evoke on its own (Holland 1984; Rescorla 1988a). Each of these and possibly other mechanisms may play a role in different cases. New tests (Rescorla 2008a) indicate that the original example of belongingness in flavor aversion and shock avoidance in rats is a case of enhanced associability between specific pairs of events. Similar experiments (Rescorla 2008b) have analyzed another example: for rats, attractive flavors are more quickly conditioned with positive consequences and bitter or sour flavors with negative consequences. Here, belongingness gives a head start to learning.

Classical associationism did recognize one kind of "belongingness." Namely, similarity and spatial contiguity between stimuli were thought to favor association formation. Of course similarity and spatial contiguity can both be seen as reasonable prior predictors of causal relationships. However, it is not always easy to disentangle them from other factors. For instance, a CS that is similar to a given US may evoke responding via stimulus generalization. But an elegant experiment with pigeons by Rescorla and Furrow (1977) shows that over and above any such effect similarity enhances associability. As indicated in Figure 4.8, all their birds were exposed to all the stimuli used in the experiment; they differed only in whether similar or dissimilar stimuli were paired in the critical second order conditioning phase. Similarly designed experiments have shown that spatial contiguity or a part-whole relation between CS and US can also facilitate second-order conditioning (Rescorla and Cunningham 1979). Although it is difficult to vary the spatial contiguity of CS to US without

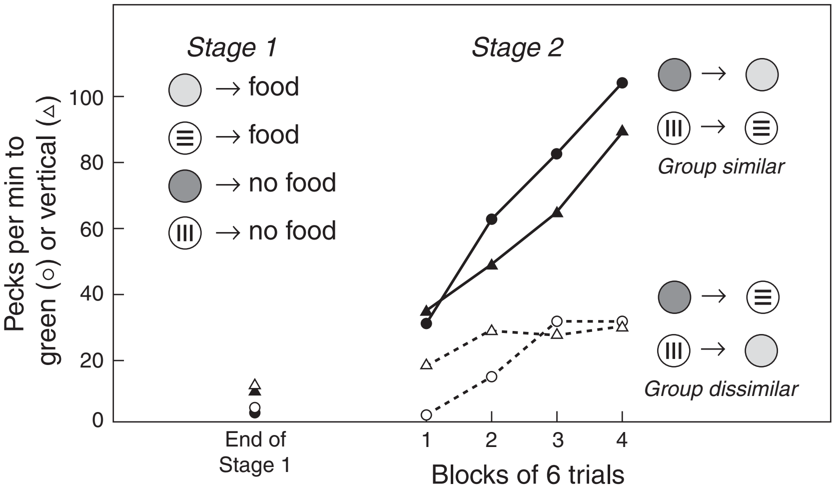


Figure 4.8. Effects of similarity between the stimuli to be associated on speed of second-order autoshaping in pigeons. Data for the end of Stage 1 are the rates of pecking the two stimuli that became CSs in second order conditioning but that predicted no food during Stage 1. The unpatterned stimuli were green and blue, shown here by dark and light shading respectively. After Rescorla and Furrow (1977) with permission.

also varying temporal contiguity, spatial contiguity by itself does appear to influence learning rate (Christie 1996; Rescorla 2008a).

4.4.5 Temporal relationships

Within limits, conditioning is more rapid the more closely in time the US follows the CS. But "close enough" depends on the CS and US. With eyelid conditioning, the CS must precede the US by no more than a second or so, whereas in conditioned taste aversion, flavor can precede illness by twelve hours or more (Box 4.1). In general, as the temporal separation of CS and US increases, conditioning improves at first but then declines (Figure 4.9). A functional reason is easy to see: causes often precede their effects closely in time and seldom follow them. However, it is easy to imagine cases in which a cause follows its effect from the animal's point of view. A stealthy predator might not be noticed until after it has attacked, but this does not mean that the victim (if it's still alive to benefit from its experience) should not learn about its enemy's features. This argument has been advanced as a functional explanation for some cases of successful *backward conditioning* (Keith-Lucas and Guttman 1975; Spetch, Wilkie, and Pinel 1981).

Figure 4.9 indicates that conditioning does not take place when CS and US are simultaneous. However, simultaneous conditioning can be quite robust in second order conditioning or sensory preconditioning, as when a pigeon associates patterns on two halves of a pecking key (Rescorla 1988a). This paradigm may capture how animals learn about the features of events, as discussed in Chapter 5. Another way to explain simultaneous and backward (as well as forward) conditioning is to suggest that conditioning establishes knowledge of the precise temporal relationship between CS and US. Indeed, Pavlov (1927) described evidence for this from the two paradigms

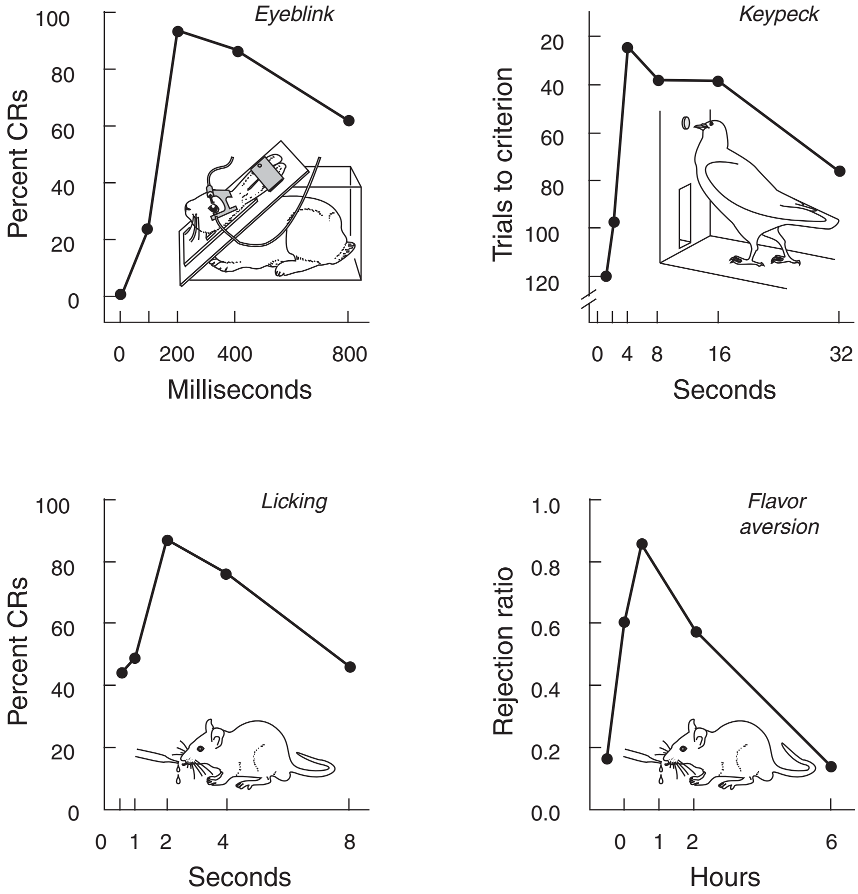


Figure 4.9. Conditioning as a function of the delay between CS and US in different conditioning preparations. Eyeblink conditioning in rabbits, redrawn from from M. Smith et al. (1969) with permission; rabbit redrawn from Domjan and Burkhard (1986) with permission; autoshaping in pigeons, data from Gibbon et al. (1977); conditioned licking with water reinforcement in rats redrawn from Boice and Denny (1965) with permission; flavor aversion in rats from Barker and Smith (1974). After Rescorla (1988b) with permission.

diagrammed in Figure 4.10. In *delay conditioning,* the CS lasted for maybe a minute or more before the food US was presented. Salivation gradually came to occur mainly near the end of the CS. Now such behavior is interpreted as evidence for timing the CS (Chapter 9). *Trace conditioning* is similar except that the CS is relatively brief and the US follows its offset by a fixed time. Hence the name: the animal is in effect conditioned to a memory trace of the CS. Evidence from humans suggests that trace and delay conditioning rely on different brain mechanisms and that trace, but not delay, conditioning depends on conscious awareness of the CS-US relationship (C. Smith et al. 2005). This suggestion has provocative implications for other species, but not all even agree on the importance of consciousness for conditioning in humans (Lovibond and Shanks 2002).

Not only the temporal pattern of events during conditioning trials is important, the time between trials—the *intertrial interval* (or ITI)—matters too. The notion that CSs provide information about the occurrence of USs suggests that when CS and US are

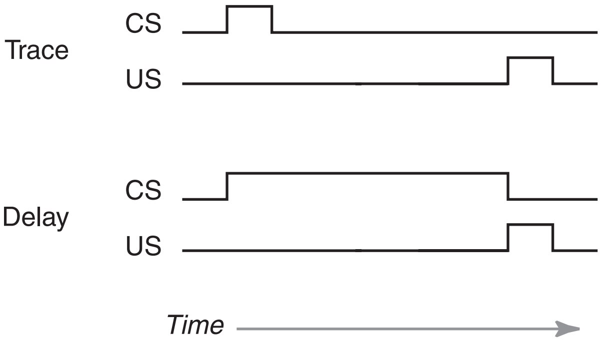


Figure 4.10. Arrangements for trace and delay conditioning.

comparatively rare, the CS is more worth learning about than when CS and US are more frequent. This corresponds to the traditional wisdom that when people learn a task *spaced practice* is more effective than *massed practice*. However, when it comes to animal training, this intuitive notion leads to a somewhat counterintuitive prediction: if for example, one is autoshaping a pigeon by turning on the keylight for 8 seconds and then presenting grain, pecking will actually appear after fewer keylight-food pairings if these trials are separated by, say, 2 minutes than by 20 seconds. It is sometimes hard for students training pigeons to accept that their bird may actually peck sooner if they don't pack the trials in too much, but in fact what matters is the ratio of intertrial time to trial time, at least in the arrangements with pigeons (Gibbon et al. 1977) and rats (Lattal 1999; Holland 2000) where parametric tests have been done. As illustrated in Figure 4.11, a higher I:T ratio, that is, longer ITI (I) relative to trial (T) or CS duration, leads to faster acquisition of responding to the CS. (This ratio is sometimes, e.g., by Domjan, 2003, equivalently referred to as the C:T ratio, where C is the "cycle time," or total ITI + CS time per trial.) A reader who has taken Section

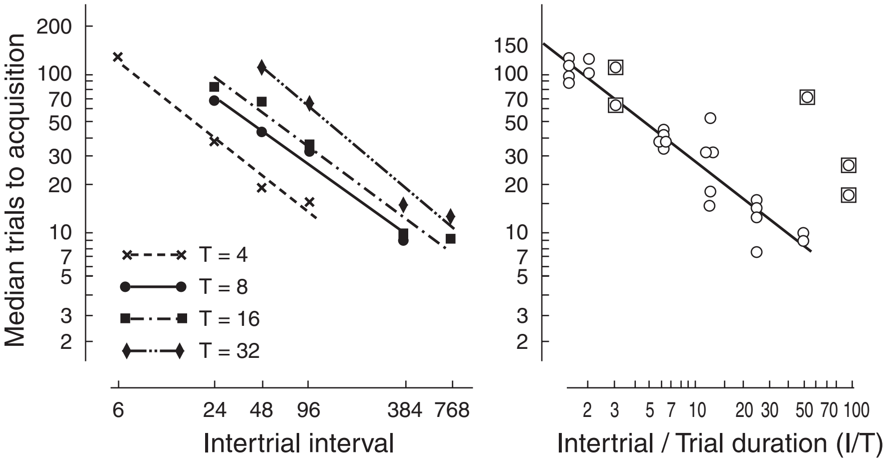


Figure 4.11. Influence of the I:T ratio on acquisition, illustrated by data from autoshaping in pigeons. Left panel shows data from groups of birds trained with the given CS (or T, i.e. keylight) and intertrial interval (ITI) durations. In the right panel the same data are replotted as a function of the I:T ratio; points in boxes were omitted in calculating the solid overall regression line . Redrawn from Gibbon et al. (1977) with permission.

4.2.2 to heart will realize that tests with a standard ITI and CS after different acquisition treatments are needed to clinch this argument. The results of such tests have been consistent with the importance of the I:T ratio for learning (Lattal 1999; Holland 2000; but see Section 4.7.2 and Domjan 2003). The implications of this and the other effects of time summarized in this section for theories of conditioning are discussed in Section 4.5.2.

4.4.6 Prior learning

In blocking, prior learning about one element of a compound CS reduces learning about the other. But the effects of past experience on present learning are more widespread. For example, exposure to a CS by itself before pairing with a US leads to *latent inhibition,* retarded conditioning to that CS. It is as if having learned that the CS signals nothing of importance the animal ceases to pay attention to it. Latent inhibition is similar to habituation, in that mere exposure to an event results in learning, but it is not clear whether the two phenomena reflect the same mechanism (Chapter 5). Exposure to the US alone in the conditioning context also reduces its effectiveness when a CS is later introduced. This can be explained as blocking of the CS by the context: the animal already expects the US, so the CS adds little new information. Conditioning to the context itself is readily observed: animals learn what to expect in particular places, be they conditioning chambers or parts of the natural environment. For example, a pigeon that has received food in a distinctively wallpapered Skinner box becomes more active when placed in that environment than in an equally familiar environment where it has never been fed. Rats learn where a novel object was located in a single trial (Eacott and Norman 2004). At least in birds and mammals, learning about the physical and temporal context of events is powerful and ubiquitous. Thinking about the role of context in learning has led to novel theoretical viewpoints (Chapter 7; Bouton 1993) as well as novel predictions about naturalistic examples of learning (Darst 2006).

If exposure to either the CS or the US alone reduces conditioning, prior exposure to random presentations of both CS and US should have an even more detrimental effect. Of course this is the random control condition. The nature of its effects is captured very well by the name *learned irrelevance* or, in the case of instrumental conditioning, *learned helplessness*. However, it is debatable whether animals actually learn that CS and US have a random relationship or whether their behavior can be accounted for by the sum of effects of CS and US preexposure (Bonardi and Hall 1996; Bonardi and Ong 2003).

4.4.7 Extinction

If conditioned responding results from learning a predictive relationship between two events, then it should be abolished if the animal has opportunity to learn that the relation no longer holds. Traditionally it was given this opportunity by removing the US and observing how the CR waned. However, the logic behind the random control condition for original learning implies that the proper way to teach an animal that CS and US are now unrelated and thereby produce *extinction* of responding is to present CS and US in a noncontingent relationship. In one dramatic demonstration of the effectiveness of this procedure, Gamzu and Williams (1971) extinguished pigeons' autoshaped keypecking by adding extra food between keylight-food pairings, preserving contiguity between the keylight and food but degrading their predictive relationship.

Extinction may appear to involve loss of a learned association, unlearning. Accordingly, Rescorla and Wagner (1972) modeled it by setting the asymptote of conditioning with no US to zero so that already-acquired associative strength decreases over unreinforced trials. However, considerable evidence indicates that, contrary to this depiction, associations are not really lost during extinction (R. Miller and Escobar 2002; Bouton and Moody 2004). *Savings* after extinction, that is, speeding up of relearning compared to initial learning, is one such piece of evidence. Another is *spontaneous recovery*, a partial recovery of extinguished responding when the animal is returned to the experimental situation, say the next day. Originally reported by Pavlov (1927), it has only been studied in any depth relatively recently and may have more than one explanation (see Section 7.3). *Reinstatement* is further evidence that learning is not entirely lost during extinction: simply presenting the US alone in the experimental context after extinction can get responding going again. Such data indicate that rather than losing the original learning during extinction, the animal acquires new learning, perhaps an inhibitory association specific to the temporal and spatial context in which extinction occurs (Bouton and Moody 2004). On this view, as in cases of memory loss which can be remedied by exposure to appropriate retrieval cues, in extinction the effects of original training are retained but need the right conditions in order to be expressed. This view is developed further in Section 7.3.

4.5 What is learned?

Saying that conditioning causes a CS to become associated with a US conceals all kinds of interesting and even contentious questions about what is learned, many of which have only begun to be unpacked relatively recently. Section 4.5.2 summarizes some of the theoretical issues involved. But first we look at some data bearing on a comparatively more straightforward question: what *is* the CS or the US from the animal's point of view, that is, what aspects of it actually enter into learning? Or, how does the animal represent the CS and the US?

4.5.1 Data

Learning about the CS

Any CS has a variety of features. It has a certain duration and intensity, it may have shape, brightness, size, loudness, taste, odor, or texture, and occur in a certain context. What is included in the animal's representation of the CS? This question can be answered by changing features of the CS after conditioning and observing the effect on responding. With CSs that can be varied along a single physical continuum like wavelength or auditory frequency, variations away from the training value often lead to orderly variations in responding as in the generalization gradients in Figure 3.9 (see also Chapter 6). Obviously, some specificity in responding is a prerequisite for concluding that conditioning has occurred at all. For example, if a rat responds in the same novel way to any and all sounds after tone-shock pairings, one would conclude that the animal was *sensitized* rather than conditioned to the tone.

As we have seen, the Rescorla-Wagner model treats separable features of a CS as if they gain associative strength independently. This makes some sense for compounds of discrete CSs from different modalities like the proverbial light + tone. But what about a compound of features from the same modality, say a red cross on a blue pecking key? Why should we think that a pigeon represents this as a blue field with a red cross superimposed on it? Maybe instead it encodes a configuration. If the key with the red cross is paired with food, the bird will come to peck it, and it might peck white keys with red crosses or plain blue keys, too. But maybe this is not because the bird has acquired a red cross association and a separate blue key association. Maybe instead the bird pecks at the red cross or the blue key alone because they are similar to the original training stimulus, that is, through generalizing from the configuration. A formal *configural model* of learning based on this intuition has been quite successful in accounting for a large body of data, including some that the elemental Rescorla-Wagner model cannot deal with (Pearce 1994b; Pearce and Bouton 2001). The relative merits of configural vs. elemental accounts of learning with complex stimuli are discussed further in Chapters 5 and 6.

Learning about time

In addition to sensory features, CSs and USs have temporal properties. The importance of temporal factors in conditioning, for example in trace and delay conditioning (Figure 4.10), was traditionally explained with the concept of the stimulus trace. For instance, the silence five seconds after a tone goes off is a different stimulus from the same silence ten seconds later because the aftereffect or trace of the tone changes systematically with time. Similarly, different times within an extended CS can be thought of as different stimuli. However, evidence that animals accurately time short intervals reviewed in Chapter 9 makes an account in terms of direct sensitivity to the durations of CSs, USs, CS-US intervals, and the like seem more natural (Savastano and Miller 1998). For instance, blocking is maximized when the CS-US interval is the same for both the pretrained and the to-be-blocked CS (Barnet, Grahame, and Miller 1993). It may seem more plausible that the CS-US interval itself is appreciated than that the traces of two qualitatively different CSs, with which the US is associated, are most similar after identical intervals, but both accounts explain this effect equally well.

The notion that the temporal relationship between CS and US is itself learned, rather than simply being one of the conditions affecting learning, suggests a novel way of viewing simultaneous and backward conditioning. Perhaps animals learn that CS and US are in fact simultaneous or in a backward temporal relationship but responding is not the same as in forward conditioning because the behavior appropriate to anticipation of an event is not the same as that appropriate to its presence or recent occurrence. As this notion suggests, rats given first order conditioning in which a tone occurred at the same time as shock showed little conditioned suppression of drinking in the presence of the tone CS, but nevertheless they acquired second order conditioned suppression when a second-order click CS preceded the tone (Figure 4.12; Barnet, Arnold, and Miller 1991; R. Cole, Barnet, and Miller 1995). There is now considerable evidence that animals learn the specific temporal patterns of events in conditioning experiments (R. Miller and Escobar 2002).

Learning about the US

When Pavlov's dog salivated to a CS for food, what had it actually learned? Did the CS evoke a complete representation of the food's taste, texture, and the like, thereby

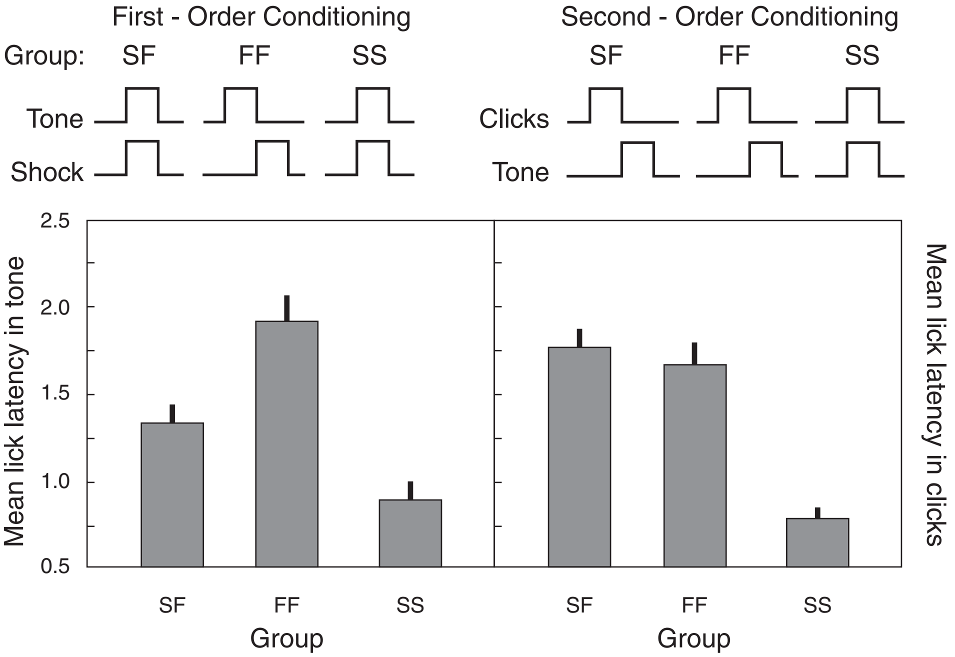


Figure 4.12. Evidence that rats learn the temporal relationship between CS and US. Three groups of rats receiving first-order and then second-order conditioning differed in whether the stimuli to be associated at each stage were simultaneous (S) or in a forward temporal relationship (F), that is, with CS preceding US as depicted above the data panels. Data from Barnet, Arnold, and Miller (1991) redrawn with permission.

causing the dog to salivate? Or did the CS evoke salivation directly? If the dog could talk, would it say "I'm salivating because I'm thinking of food" or would it say "This tone makes me salivate, but I don't know why?" A classic demonstration that animals encode the features of reward comes from instrumental learning, a delayed-response experiment by Tinklepaugh (1928). Monkeys saw a piece of their favorite banana or less-preferred lettuce being hidden. After a retention interval, the animals were allowed to uncover the reward and eat it. When lettuce was substituted for banana on occasional trials, the monkeys showed signs of surprise and anger, indicating that they knew not simply where the reward was but what food it was (Figure 4.13). Watanabe (1996) repeated such observations using an operant task and recorded distinct patterns of cortical activity corresponding to the monkeys' expectations of raisin, apple, cabbage, water, grape juice, and other rewards. The implications of such findings for the cognitive structure underlying instrumental behavior are discussed in Chapter 11.

Questions about how the US is represented can be addressed in Pavlovian conditioning by changing the value of the US after training. If responding is unaffected, the animal must have merely associated the CS with the response or response system activated by the original US. Often, however, responding changes with postconditioning changes in the value of the US in a way that indicates the animal has associated the CS with a detailed representation of the US. For instance, the value of a food to rats may be decreased by pairing it with poison. The rats then show less conditioned

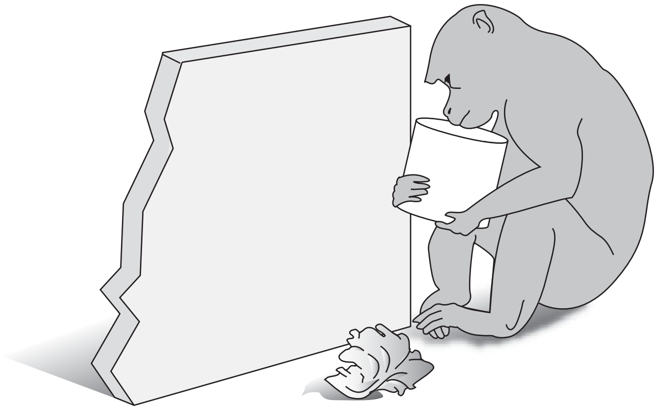


Figure 4.13. Tinklepaugh's monkey Psyche looking for banana when lettuce had been secretly substituted. After a photograph in Tinklepaugh (1928).

responding to a CS previously paired with that food than do control rats given noncontingent poisoning. Such tests must be done without further USs being given (i.e., in extinction) so as to tap the representation established by the original training rather than new learning that the CS signals nasty food (Holland and Straub 1979).

A similar technique can be used to discover which sensory features of the US are encoded. For instance, rats can be trained with two different CSs, each paired with a distinctive type of food, say food pellets and sucrose. If the rat represents both USs merely as "food," "something tasty," or the like, then it should not matter which of them is later paired with poison: conditioned responding should decrease to the CS signaling either one. In fact, however, responding decreases selectively to the CS whose US was devalued (Colwill and Motzkin 1994; Colwill 1996). Selective satiation or deprivation also change US value. For instance, pigeons that are hungry but satiated with water reduce pecking at a CS signaling water but not at one signaling food (Stanhope 1989). However, after extended training responding may continue at a high rate even though the reinforcer has been devalued. Animals apparently learn about both the sensory and the affective or response-eliciting features of USs, perhaps to different degrees in different circumstances (Dickinson 1980; Balleine and Dickinson 2006).

Images of the US

So far, this section indicates that a CS evokes a representation of a particular US, an image of the US in some sense. As this idea suggests, associatively evoked stimulus representations can substitute for the stimuli themselves in new learning (Holland 1990; Hall 1996). In one demonstration (Holland 1990), rats were exposed to pairings of a tone with food until they showed clear evidence of anticipating food in the presence of the tone. The tone was then paired with injections of a mild toxin, a toxin adequate to condition aversion to any distinctive flavor paired with it though not to the tone itself (see Box 4.1). As a result of the tone-toxin pairings, the rats developed an aversion to the food previously paired with the tone. It was as if during these pairings the tone evoked an image of the food and that image was associated with toxin (Dwyer 2003; Holland 2005).

Such learning about absent events turns out to be quite robust, and it need not involve flavor aversions. For example, Holland and Sherwood (2008) trained individual rats with one light signaling a tone and a second light signalling sucrose. After subsequent training in which the "tone light" signaled the "sucrose light," the rats investigated the food cup more during the "tone light" than did control rats. Two previously learned CSs can also serve as surrogates for their associates in inhibitory learning (Holland and Sherwood, 2008). Such findings are important because they suggest that conditioning allows animals to bring absent events to mind and acquire new information about them, a primitive form of thought (Holland 1990; Hall 1996).

4.5.2 What is learned? Theory

S-S or S-R associations?

Historically, the question "What is learned in conditioning?" was posed as "Are associations formed between CS and US (stimulus-stimulus, S-S, associations) or between CS and UR (stimulus-response, S-R, associations)?" The 1940s and 1950s saw numerous experiments designed to determine whether learning consisted of S-S or S-R connections, mainly using instrumental learning. In experiments with mazes, this amounted to the question whether animals learned a rigid response such as turning right or acquired knowledge about the location of the goal, a cognitive map which they could use to reach the goal in different ways as circumstances required (Chapter 8). As usual in controversies of this kind, the answer seemed to be "it depends," in this case on factors like the amount and conditions of training. The S-R versus S-S distinction is often phrased for Pavlovian conditioning as a distinction between *procedural* and *declarative* learning. Does the animal merely learn what to do in the presence of the CS (S-R or procedural learning) or does it form a representation that could be expressed as a proposition, "A is followed by B," and base action on this knowledge in a flexible way (S-S or declarative learning)? The experiments discussed in the last section, in which the value of the CS or the US is changed after training, have shown that either may occur and that S-S learning may include quite a detailed representation of both CS and US.

More than associative strength?

A more fundamental question than whether associations are S-S or S-R is whether what is learned in conditioning is best conceptualized as associations at all. An important condition for learning is the temporal patterning characteristic of contingency between events, so why not conclude that this is what animals learn? Gallistel (1990; Gallistel and Gibbon 2000) suggested that animals record the times of onset and offset of potential CSs and USs and compute whether the statistical likelihood of the US increases during the CS. Responding is determined not by stored associative strength but by an online computation of the statistical uncertainty about whether the US will follow the CS. This analysis is useful because it formalizes the notion of contingency. However, the fact that a theorist can compute contingency in this way does not mean that animals must do the same computations in order for their behavior to reflect the contingencies they experience. Sensitivity to the sorts of experiences afforded by conditioning experiments may have evolved to enable animals to track causal, or contingent, relations among events in the environment, but an animal that blindly forms associations by contiguity in the way described by the Rescorla-Wagner model can track causality or contingency very well without having any representation of causality or contingency as such. There is an important general caveat here: cognitive mechanisms do not necessarily embody literal representations of their functions, and assuming that they do can blind us to what is really going on (see also Chapter 2 and p. 82 in R. Miller and Escobar 2002). In Chapter 12, for instance, we see that some animals may behave as if sensitive to the states of mind of their companions but without representing others' states of mind as such at all.

RET and the comparator model

Nevertheless, Gallistel (1990) and others (R. Miller 2006) have correctly pointed to a serious problem: an association as traditionally conceived has only one dimension, strength. Thus it cannot encode the temporal relationship between CS and US, even though it is clear that animals learn this (section 4.5.1). Moreover, increasing evidence from studies of animal memory (Chapter 7) lends plausibility to the claim that animals remember the details of a large number of the individual episodes experienced in a conditioning experiment. This flies in the face of the implicit assumption that all that is acquired in conditioning is a connection that summarizes past experience with a particular CS and US in a single value of associative strength. The Rescorla-Wagner model and its variants also assume that associations of the same strength acquired in different ways are equivalent. This assumption of *path independence* is clearly not always correct (R. Miller, Barnet, and Grahame 1995; R. Miller 2006). For instance, an equally weak CS-US association could be present early in training or after extinction, but further training would proceed faster after extinction than it did originally, indicating that the animal has retained some effect of the original training that is not evident in performance of the CR.

Such evidence that animals acquire more complex and detailed information than can be encoded in unidimensional associations has stimulated formulation of two distinct alternative models in which animals retain a more or less veridical representation of the events during conditioning, including their temporal properties. Performance is determined by an online comparison of some sort, making these models fundamentally different from the Rescorla-Wagner and related models in which performance directly reflects the strength of learning (Dickinson 2001a; Gallistel and Gibbon 2001; R. Miller and Escobar 2002). That is, they are performance-based rather than acquisition-based models (R. Miller and Escobar 2001). In the comparator model developed by Miller and his group (see R. Miller and Escobar 2002) learning is through simple contiguity. During a blocking experiment, animals do associate the added (blocked) CS with the US. At the test the animal compares the strength or predictive value of the added CS to that of other CSs present or associated with it and finds that the CS trained first has a stronger link to the US. This point of view predicts *backward blocking* (or *retrospective revaluation*). That is, rather than blocking CS B by training A-US and then AB-US, one trains AB-US first and then, in effect, teaches the animal that A was actually the cause of the US by training A-US. Indeed, as the informal description of this procedure suggests, in the final test of B animals may show little conditioned responding, as if they do not attribute the US to it. However, it is possible for a modified acquisition-based model to account for such effects (see R. R. Miller and Escobar 2002).

Similarly, in Gallistel and Gibbon's (2000) rate expectancy theory (RET), performance is based on an ongoing comparison of the rate of USs during the CS with their rate overall, that is, during CSs plus ITIs. This view predicts that the distribution of total CS experience across trials should be unimportant. For example, if training consists of episodes with 100 seconds of ITI and 20 seconds of CS per US, it shouldn't matter whether the animal experiences 100-second ITIs and 20-second CSs, each followed by a US or 50-second ITIs and 10-second CSs, half of which end in a US (i.e., partial reinforcement, which is usually supposed to retard acquisition (Gottlieb 2005). In either case, the relevant rates will be one US per 20 seconds when the CS is present and one US per 120 seconds overall. Several well-controlled tests of such a prediction have, however, produced results more consistent with the traditional trial-based account of acquisition, though sometimes revealing an additional role for time (e.g., Bouton and Sunsay 2003; Domjan 2003; Gottlieb 2005).

Contrary to the traditional assumption that associative strength increases gradually over trials, RET implies that number of trials, that is, CS-US pairings, as such is unimportant. Tests of this prediction have tended to support RET over trial-based approaches. As one example, a review of acquisition data from a variety of species and conditioning paradigms reveals that individual animals abruptly switch from responding hardly at all to responding at close to their asymptotic rate instead of increasing responding smoothly over trials (Gallistel, Fairhurst and Balsam 2004). Group learning curves resemble the theoretical curve of associative strength in Figure 4.6 only because they average individual curves. However, models based on associative strength can account for such findings by postulating a threshold of associative strength above which the animal always responds. In an even more direct test of the importance of number of trials, Gottlieb (2008) compared acquisition of conditioned approach to a food dispenser (magazine) in rats or mice given either 4 or 32 trials, when trials were distributed within and between sessions so as to equate either total ITI or total session length across groups. Little effect of the eightfold increase in trials was evident in training sessions and, most importantly, in a common test at the end of training. According to RET, this is because only a trial or so is necessary to give the animal evidence that the CS predicts the US; the rest of the session shows it that the context alone does not.

Summary

The twenty-fifth anniversary of the Rescorla-Wagner model occasioned major assessments of its successes and limitations (R. Miller, Barnet, and Grahame 1995; Siegel and Allan 1996). In the ensuing years, arguably some problems with it have become more acute (R. Miller 2006). Among the areas considered in this book, conditioning is one for which formal modeling is particularly well developed. The Rescorla-Wagner model has guided discovery of new phenomena and still summarizes much of what we know (Pearce and Bouton 2001), but newer alternatives imply that the analysis of conditioning can and should be better connected with other aspects of animal cognition, in particular timing and memory. As illustrated in the preceding few paragraphs, they have also stimulated researchers to examine some fundamental associationist assumptions. One review (R. Miller and Escobar 2002) characterizes theory development in this area as a continual tension between simple and easily falsifiable models vs. more elaborate models devised to deal with the problems of the simple ones. It remains to be seen whether any single model will eventually prove adequate to all the richness and variety of phenomena that current debates are revealing. This includes phenomena of human causal or contingency learning in associative paradigms, which are largely beyond the scope of this book, but some of which seem more compatible with the acquisition of propositional knowledge than simple excitatory or inhibitory links (De Houwer 2009; Dickinson 2009).

4.6 Conditional control of behavior: Occasion setting and modulation

Consider the following problem, known as a *feature positive discrimination:* In the presence of stimulus A nothing happens, but when A is preceded by another stimulus, X, the US follows A (Figure 4.14). The Rescorla-Wagner model predicts that conditioning will accrue only to X because it is the only reliable predictor of the US. Stimulus A should gain no strength because the US occurs whether or not A is presented. This is indeed what happens if X and A are simultaneous. However, if X and A are presented serially, so that X precedes reinforced occurrences of A while A alone is not reinforced, X does not become an excitor. Rather, it acquires the ability to modulate excitation to A. The serial feature positive discrimination appears to support a different, higher-level, kind of learning from the simple excitatory or inhibitory connections between event representations discussed so far. This kind of learning has been called, alternatively, *facilitation,* by analogy with inhibition, whose conceptual opposite it appears to be (Rescorla 1987), and *occasion setting,* by analogy with the occasion setting function of discriminative stimuli in instrumental learning (Holland 1992), or simply *modulation* (Swartzentruber 1995). A stimulus can be simultaneously an excitor and a modulator, and these functions are somewhat independent.

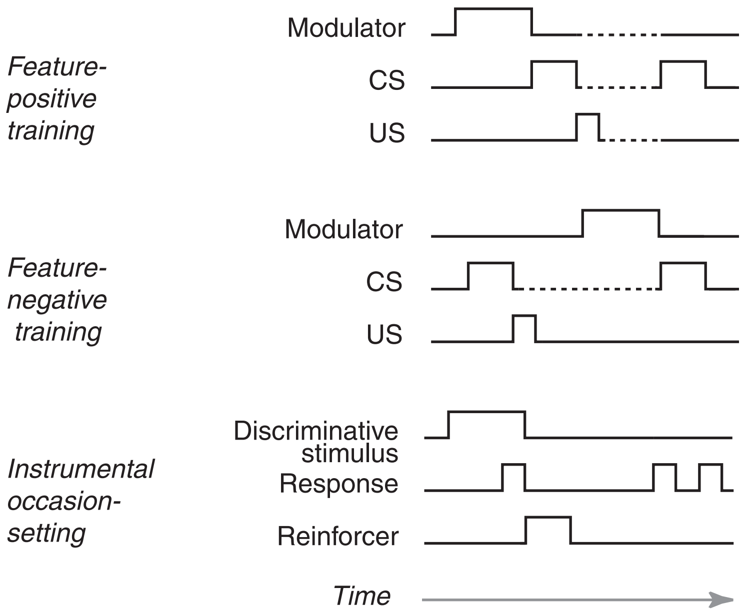


Figure 4.14. Procedures for training Pavlovian modulators and instrumental occasion setters. Each row shows one trial with and one without the modulator/occasion setter.

Two kinds of evidence show that modulation is not the same as simple excitation: First, modulation has different conditions for acquisition and extinction. Second, excitors and occasion setters fail to block each other, indicating that the contents of learning are different. For instance, continuing the example above, the necessary condition for extinction of facilitation is that X predict nonreinforcement of A. Simply presenting the facilitator alone, with no reinforcement and no occurrences of A, does not extinguish its facilitatory function (Rescorla 1986). One of the two traditional paradigms for demonstrating Pavlovian conditioned inhibition (Rescorla 1969) parallels that for training a facilitator: a CS is reinforced when presented alone but nonreinforced when preceded by another stimulus, the conditioned inhibitor. It now appears that conditioned inhibitors trained in this way (as opposed to those trained with simultaneous presentations with the nonreinforced CS) are best viewed as modulators with properties analogous to those of facilitators (i.e., positive modulators Williams, Overmier, and LoLordo 1992; Swartzentruber 1995).

Modulation has been investigated in several different preparations, sometimes with different results (see Pearce and Bouton 2001). What is clear is that facilitation differs from simple conditioning in a number of ways. It seems to develop in parallel with excitation and to serve a kind of higher-level function that is not readily captured by simple associative models of conditioning. Moreover, although it has been useful to study modulation using discrete stimuli, it is clear that environmental contexts are important modulators of associative information in addition to becoming directly associated with CSs and USs (Bouton 1993; Swartzentruber 1995; Pearce and Bouton 2001). The most important feature of modulation or occasion setting is that it allows animals to use associative information in a flexible and appropriate way rather than mindlessly performing a CR whenever a CS appears.

4.7 Effects of learning on behavior

4.7.1 Learning and performance

On the view that Pavlovian conditioning is merely transfer of control of a reflex, S-R learning, behavior automatically results from learning so there is no distinction to be made between learning and performance. However, examples of "behaviorally silent learning" (Dickinson 1980) compel a distinction between learning and performance. As one example, inhibitory learning, that is, below-zero associative strength in Rescorla-Wagner terms, may not become evident until the conditioned inhibitor is presented in combination with an excitor and suppresses conditioned responding (Rescorla 1969). In another example, Holland and Rescorla (1975) presented food to rats following either a tone or a light. The rats soon became more active during the tone, but activity changed very little during the light, suggesting that the rats had learned only about the tone. Nevertheless, when rats trained with the light had second order conditioning in which the tone predicted the light, they became more active to the tone. The light could also block first-order conditioning to the tone. Eventually direct observations (Holland 1977) revealed that the rats' behavior did change during the light, but not in a way that influenced motion of the jiggle cage that Holland and Rescorla (1975) had used to record general activity. In fear conditioning, too, rats show different CRs to tones and lights that support the same underlying learning (Kim et al. 1996). In such cases, learning is "silent" until it is measured appropriately.

If learning is distinct from performance, then *performance rules* are needed to describe how learning is expressed in behavior. The traditional Pavlovian performance rule was *stimulus substitution:* the CS becomes a substitute for the US. A dog salivates when fed, so it salivates to a signal for food. Pigeons that are both hungry and thirsty peck a lighted key signaling food in the same way as they peck at food, whereas they "drink" a key signaling water (Jenkins and Moore 1973). But much of the behavior resulting from Pavlovian conditioning is not strictly stimulus substitution. For example, if rats see another rat passing by on a trolley just before food arrives, they don't try to eat the signal rat but exhibit social behaviors like sniffing its face and crawling over it (Timberlake and Grant 1975). Hamsters, which would not normally interact socially over food, do not develop any social or feeding behavior in such a situation (Timberlake 1983).

Such findings can be roughly described by saying that species-specific behavior appropriate to the US occurs during the CS if there is stimulus support for it. Thus, diffuse visual stimuli paired with food cause pigeons to become active rather than to peck. Shock generally makes rats jump and squeak, but after getting shock from touching a small prod rats throw sawdust over the prod and bury it, whereas they freeze (i.e., become completely inactive) in the presence of diffuse signals for shock to the feet (Pinel and Treit 1978). Behavior in such cases is determined by the nature of the CS itself, not merely by what stimuli happen to be present when it appears. This is shown very clearly by observations of rats' behavior to a compound of a light plus a tone CS for food (Holland 1977). Rats pretrained to the light (i.e., rats for which conditioning to the tone was blocked) behaved in a way appropriate to the light when the light and tone were presented together, whereas rats pretrained to the tone behaved as they normally did with the tone alone. Some differences in CR form can be accounted for as enhanced orienting responses to the CSs involved (Holland 1984), but as we see below the preexisting natural relationship between CS and US may also be important.

4.7.2 Behavior systems

Can all the different kinds of CRs animals display be described in a unified way that allows unambiguous predictions for new species and situations? An approach based on the ethological notion of behavior systems introduced in Chapter 2 reasonably hypothesizes that the CS brings into play the behavior system relevant to the US (Holland 1984; Suboski 1990; Hogan 1994b; Hollis 1997; Timberlake 2001b; Domjan 2005). Because behavior systems can be assessed outside of conditioning situations, this approach offers a powerful causal analysis of conditioned behavior (Shettleworth 1994a). In terms of the model of a behavior system in Figure 2.7, Pavlovian conditioning could result in modification of either perceptual-motor or perceptual-central connections. Perceptual-motor connections correspond to S-R learning: the CS triggers a particular movement, as in stimulus substitution. However, conditioning often seems to result in new perceptual (CS)—central connections that facilitate the whole system of behaviors relevant to the US (Hogan 1994b). Behavior systems may also have a temporal organization, with activities that change with proximity to the relevant goal as illustrated in Figure 4.15 and discussed further below.

Behaviors shown after conditioning have a preexisting organization that influences their performance as CRs. For example, pigeons normally peck only stimuli much smaller than the usual 2.5 cm. diameter pecking key. If a 6-mm. dot, smaller than the pigeon's gape, is on the key in an autoshaping experiment, pecking develops

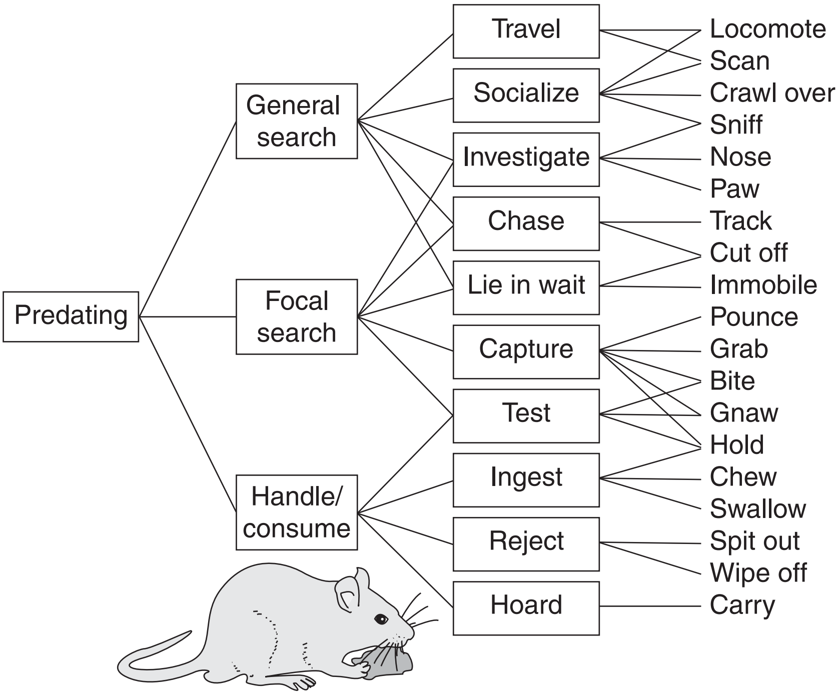


Figure 4.15. The organization of the rat's feeding system. The three functional subsystems indicated are activated in the order shown from top to bottom as the rat searches for and then finds food. Redrawn from Timberlake (1994) with permission.

to it much more quickly than to the blank key (Jenkins, Barnes, and Barrera 1981). In the behavior system view, this illustrates the joint control of a CR by its normal causal factors (the size of spots) and associative ones. The behavior systems account also explains why CRs are not necessarily the same as URs. For instance, when young chicks are placed in a cool environment and exposed to pairings of a lighted pecking key and a heat lamp, they come to peck the key even though they never peck the heat lamp (Wasserman 1973). If the lamp is seen as a surrogate mother hen, the CR of pecking can readily be understood: chicks peck at the mother's feathers and snuggle underneath her as she sits down to brood them (Hogan 1974). The behavior system view also implies that not all species will show the same CRs in a given situation. For instance, how seven species of rodents treat a moving ball bearing that signals food depends on their species-specific predatory behavior (Timberlake and Washburne 1989).

4.7.3 Behavior systems and the function of conditioning

The behavior systems approach offers a causal analysis of what animals do in conditioning experiments, but much research based on it has also been guided by thinking about the functions of conditioning in the natural lives of animals. This thinking has led to some novel predictions and discoveries. For example, on the view that the function of conditioning is to allow animals to learn cause-effect relationships, the CR should optimize the animal's interaction with the US (Hollis 1982; Hollis 1997; Domjan 2005). This is not an answer to Tinbergen's mechanism or development question but to the current function question. It does not mean that CRs are instrumental responses learned through reward and punishment. Indeed, *omission training* experiments show that CRs may occur despite adverse experimental consequences, as if they are involuntary. For instance in autoshaping pigeons go on pecking even if pecking cancels food (Chapter 11). Evidence from conditioning with USs including drugs, shock, and sexual behavior shows that this functional approach makes sense of a wide variety of CRs (Hollis 1997; Domjan 2005). Importantly, this includes cases of conditioning with drugs where the CR is opposite rather than similar to the UR. A CR of vasodilation may occur when the direct response to the drug (the UR) is vasoconstriction, body warming occurs instead of cooling, and so forth. Such CRs maintain homeostasis by counteracting a drugs' tendency to push physiological variables outside normal ranges (Siegel 2005). Such *compensatory* CRs make sense in the same framework as stimulus substitution: both function to optimize interaction with USs.

The notion that the tendency to display particular CRs evolved because they contribute to fitness suggests testable predictions about the present-day function of conditioning. For example, Hollis has shown that sexual and aggressive CRs do in fact give some fish an advantage that is very likely to translate into reproductive success, and in one case she and her colleagues measured reproductive success directly. Male blue gourami fish (*Tricogaster tricopterous*) were trained to expect an encounter with a territorial rival following lighting of a red panel on the side of their tank. The fish evidenced knowledge of the predictive relationship between the panel and the rival's arrival by displaying aggressively during the CS (Figure 4.16). Control males had either unpaired exposure to rivals and the red panel or exposure to rivals alone. When pairs of conditioned and control males were shown the red panel at the same time and then allowed to fight each other, the conditioned males showed more bites and tailbeating responses than their rivals, and they nearly always won the fights (Hollis 1984; Hollis et al. 1995).

A provocative illustration of how conditioning contributes to social behavior comes from a similar experiment with blue gouramis, this time involving competition for food between two nonterritorial males (Hollis et al. 2004). Pairs of males were first observed as they formed dominance relationships, in which the dominant usually

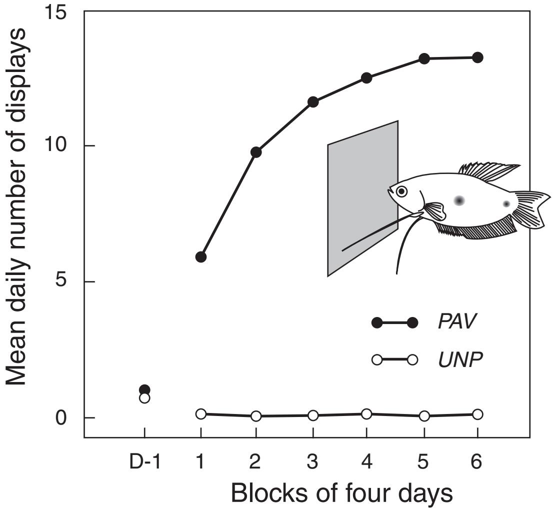


Figure 4.16. Male blue gouramis' aggressive display toward a light paired with a rival (Pav group) and in an unpaired (UNP) control group. Redrawn from Hollis (1984) with permission.

won contests over food. Then the males of each pair were separated and each was exposed to a small light CS signaling food dropped into the tank. Conditioned males oriented toward the light when it came on, approached it, and nipped at the water surface, whereas in control males these behaviors waned with unpaired light-food experience. However, when dominant and subordinate males were put together for tests, on the very first trial subordinate males trained with light-food pairings did not perform their previous suite of CRs. Instead, before the dominant had time to attack they adopted a submissive head-up posture. Thus, by anticipating food in the presence of the dominant, whether that dominant himself was conditioned or not, subordinates reduced the number of attacks and bites they were subjected to. In some cases they were actually able to steal some of the food. This example of behavioral flexibility in conditioning is worth keeping in mind when we come to discuss the cognitive basis of social tactics in Chapter 12.

Breeding males of many species behave aggressively toward any animals approaching their territory, even females. If the male could anticipate the approach of a female and inhibit undue aggression, mating success might be increased. Indeed this has proven to be the case in blue gouramis. Male blue gouramis' sexual behavior can be conditioned with a female as a US using methods similar to those for conditioning aggressive behavior (Hollis, Cadieux, and Colbert 1989; Hollis 1990). After presentations of the CS, conditioned males direct fewer bites and more courtship movements at a test female than do controls; that is to say, the CS prepares them for mating. Moreover, this behavior translates into spectacularly enhanced reproduction. When conditioned and control males remained with females after a single presentation of the CS, the conditioned males spawned sooner and fathered on average over a thousand young, compared to a mean of less than 100 fathered by controls for which the CS had been explicitly unpaired with a female (Hollis et a1.1997). Similarly when male Japanese quail (*Coturnix japonica*) mate in a chamber where they have previously encountered females, they release more sperm than do control males (Domjan, Blesbois, and Williams 1998), and their partners produce more fertilized eggs (Adkins-Regan and MacKillop 2003). Females conditioned in a similar way also produce more eggs after copulating in the presence of the CS for mating (Adkins-Regan and MacKillop 2003; Mahometa and Domjan 2005). And when two males in succession copulate with a female in a context that is a sexual CS for one of them, the conditioned male fathers more of the resulting young, that is, he has an advantage in sperm competition (Matthews et al. 2007).

4.7.4 Behavior systems and the laws of learning

The typical measure of strength of learning is the probability or intensity of a single CR. Thus, the low levels of CR performance with long CS-US intervals (Figure 4.9) or with a low I:T ratio (Figure 4.11) have been taken as evidence of poor learning. But the behavior systems approach suggests that although responses resembling consummatory behavior may not be seen under these conditions, general search activity might increase in the experimental context. This idea has proven useful in accounting for the CRs shown with CSs of different durations in conditioning of fear in rats (Fanselow 1994), feeding in rats (Timberlake 2001b), and sexual behavior in quail (Domjan, Cusato, and Krause 2004). In all three systems, conditioning is evident even with quite long CS-US intervals, but what CR appears depends on the interval. The influence of CS-US interval on CR form has long been recognized, for instance in Konorski's (1967) distinction between preparatory and consummatory CRs. In his terms, preparatory behaviors tend to be shown with long CS-US intervals and consummatory behaviors with short ones. In the behavior systems account, the behaviors within appetitive systems such as feeding or sex are classified functionally as general search (e.g., general activity in search of food or a mate), focal search (e.g., striking and pouncing on prey; grabbing and mounting a female), and consummatory behaviors (e.g., tearing and chewing prey, ejaculating; Timberlake 1994, 2001b). Similarly, the perceived imminence of attack determines which defensive behaviors are shown (Fanselow and Lester 1988). Preencounter behaviors such as reorganization of feeding or increased vigilance occur in places where predators have been encountered before, an animal that has just met a predator engages in postencounter behaviors like freezing or fleeing, but if the predator attacks, the victim shows circa-strike behaviors such as vocalizing and striking back at its attacker.

As an example, consider the studies of Domjan and his colleagues (Domjan, Cusato, and Krause 2004; Domjan 2005) with Japanese quail (*Coturnix japonica*). In these studies, male quail typically receive one trial per day in a large chamber with a US consisting of opportunity to copulate with a receptive female kept in an adjacent chamber. Akins (2000; see also Domjan, Cusato, and Krause 2004) trained birds with 1-minute or 20-minute presentations of a CS consisting of a terrycloth-covered object roughly the size and shape of the body and neck of a female quail (see Figure 4.17). At each CS duration, birds for which the CS immediately preceded access to the female were compared to unpaired controls who copulated two hours before CS presentations. Birds trained with the short CS quickly increased the time they spent near the CS object during the first minute it was present, whereas those trained with the long CS increased their activity, or general search, above control levels. Importantly, both CRs appeared within just two or three trials. In Akins's (2000) experiment, both the 20-minute and the 1-minute CSs were exceptionally short relative to the ITI, since the subject birds actually spent the entire 24 hours containing each trial in the conditioning chambers. However, when Burns and Domjan (2001; Domjan 2003) varied the I:T ratio by varying the time the birds spent in the chambers, they still found strong learning at what should have been an unfavorable ratio, but it was evident in general activity rather than approach to the CS. Rats show comparable effects during conditioning with food (Silva and Timberlake 1997). Even in conventional conditioning arrangements, variation in CS-US interval may have different effects on different measures of learning (Delamater and Holland 2008). Such findings cast doubt on the

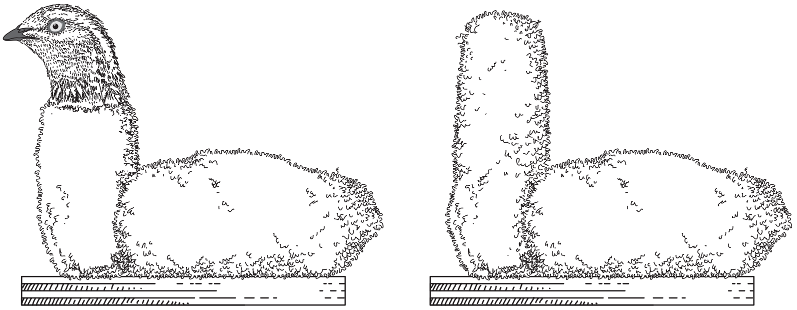


Figure 4.17. More and less quail-like objects used as CSs in sexual conditioning of male quail in the studies by Akins and by Cusato and Domjan. Redrawn from Cusato and Domjan (1998) with permission.

claim (Section 4.4.5) that the I:T ratio is a critical determinant of the strength of conditioned responding (Domjan 2003).

As we have seen, the behavior systems approach predicts that CRs will depend on the species-specific relationship of the CS to the behavior system relevant to the US. In one of the most comprehensive analyses of such effects, Timberlake and colleagues (see Timberlake 2001b) showed, for example, that for rats rolling ball bearings versus conspecifics on trollies versus diffuse lights and tones all result in predictably different CRs with the same food US. Similarly, in sexual conditioning with quail (Domjan, Cusato, and Krause 2004; Domjan 2005) localized lights, diffuse context cues, and different sorts of quail-sized objects all support different CRs. Earlier, we saw how Holland (1977) found that in rats conditioned with food, lights and tones support different CRs expressive of the same underlying learning, as revealed by blocking and second order conditioning. However, some of the research by Timberlake and Domjan suggests that naturalistic CSs may actually support qualitatively different learning which cannot be blocked by more arbitrary CSs.

As an example, consider some of the findings with quail (for review see Domjan, Cusato, and Krause 2004). Because these birds live naturally in short grassland, a male would often see a female's head and neck as she approaches before getting close enough to copulate. This bit of natural history suggested using as a CS the object with the head and neck of a female quail shown in Figure 4.17 along with a control CS of the same shape and size (Cusato and Domjan 2000). Both objects therefore afford males the opportunity to mount and attempt to copulate. When they were used as CSs, conditioned approach behavior exceeded levels in unpaired controls with either one, but grabbing, mounting, and attempts at cloacal contact with the model exceeded control levels only in the group trained with the more realistic model. By itself the superiority of this model could reflect an effect purely on performance, and the response of naïve males showed that it is indeed more effective in eliciting sexual responses. However, a study of blocking (Figure 4.17; Koksal, Domjan, and Weisman 1994) suggests that it actually supports stronger underlying learning. Quail were first conditioned with a localized light predicting copulatory opportunity. They revealed their learning by approaching the light when it came on. Controls had either unpaired light and copulation experience in the first phase or no training. Then all birds received four trials in which one of the models shown in Figure 4.17 was lowered into the cage at the same time as the 30-second light came on. Blocking and control groups trained with the naturalistic model spent high proportions of the trial near it, that is, the light CS did not block learning with this model, but it did block conditioning to the model lacking the head and neck of a female quail.

Domjan (2005) suggests that conditioning with the more realistic model exemplifies a widespread natural situation in which the CS has a preexisting relationship to the US, perhaps because it is part of the US (as with the quail model) or because it is a natural precursor of the US, as for a baby mammal contact with a mother's nipple is a natural precursor to obtaining milk. The failure of blocking just described, as well as effects of the I:T interval and other evidence that learning with the naturalistic quail CS is especially strong and supports more US-appropriate CRs, suggests that such naturalistic contingencies support learning that obeys different principles than learning with the traditional arbitrary CSs (Timberlake 2001a; Domjan, Cusato, and Krause 2004). Quite separately from the behavior systems approach, on the basis of other evidence Miller and colleagues (Oberling et al. 2000; R. Miller and Escobar

2002) suggest that in general stimuli of high inherent or acquired biological significance are protected from overshadowing and blocking. In their terms, high biological significance is equivalent to strong preexisting responses to the candidate CS. Although this may boil down to the same thing suggested by behavior systems, it seems less satisfactory because it lacks the same connection with the functional organization of behavior, a connection which has been used to predict and explain some intriguing phenomena.

4.8 Concluding remarks

This chapter began with some general ideas about the function and evolution of learning. The section on Pavlovian conditioning sketched three different sets of ideas that closely connect theories of the mechanism of conditioning with assumptions about its function. Traditionally, conditioning is seen as a mechanism for associating effects with their causes. This view has roots in philosophy. It is echoed today in associative accounts of experiments on human causal reasoning (Baker, Murphy, and Mehta 2001) and is the basis for modeling the effect of conditioning as a change in associative strength. Such models implicitly assume that the content of associative learning is excitatory and inhibitory links between event representations with no representational content themselves. The RET model emphasizes the importance of conditioning for tracking patterns of arbitrary events through time and proposes a mechanism by which animals explicitly do this. The behavior system approach, as we have just seen, focuses instead on natural signaling relationships. In nature, CSs may be precursors to, or even parts of, USs and the function of conditioning is to optimize interaction with those USs. Each of these views inspires distinctive kinds of experiments instantiating situations in which learning has its assumed function. But the mechanism of learning need not directly reflect this function. In all cases, the function of learning is ultimately to allow animals to adjust behavior appropriately to forthcoming events. It remains to be seen whether and, if so, how different contemporary views about how this happens can be harmonized.

In addition to the basic facts about Pavlovian conditioning, this chapter has two lessons to keep in mind for the rest of the book. One is that the conditions for learning, the contents of learning, and the effects of learning on behavior are central to a behavioral analysis of any kind of learning. The review of Pavlovian conditioning that takes up most of the chapter shows how these three basic questions have been addressed in one very well studied case. It thus provides a model for analyzing other forms of learning. Secondly, even in this apparently simple form of learning, animals show evidence of subtle and interesting cognitive processing. For instance, rats or pigeons learn about multiple features of CSs and USs, the context in which they occur, and the temporal relationships between them. Access to some of this information is conditionally controlled by the context, so that only the information most relevant in the current situation controls behavior. Thus associative learning is not a stupid, low-level, process to be contrasted with more "cognitive" mechanisms. It is important to keep in mind the power of conditioning to produce subtle and sophisticated adjustments to the local environment when evaluating claims that some examples of adaptive behavior require other mechanisms for their explanation.

Further reading

A comprehensive introduction to Pavlovian and instrumental conditioning is the text by Bouton (2007). The textbooks by Eichenbaum (2008) and by Gluck, Mercado, and Myers (2008) combine introductory surveys of research on conditioning and learning with introductions to related neurobiological research. Higher-level reviews of all these topics can be found in volume 3 of Stevens' *Handbook of Experimental Psychology* (Gallistel 2002). An excellent comparative survey of learning and its neurobiological basis can be found in the relevant chapters of Papini's (2008) text. The function and evolution of learning, with particular reference to insects, is also discussed in the chapters by Dukas (2008, 2009).

5

Recognition Learning

To recognize is *to know again,* "to perceive to be identical with something previously known" (*Oxford English Dictionary,* 3rd edition). Therefore, in a sense all learning involves recognition. This chapter is about how animals learn about objects, other animals, and events they experience in the absence of obvious relationships with other events. Such learning seems to reflect what people usually mean by *recognition.* When I ask, "Do you recognize that woman?" I mean "Have you seen her before?" Psychologists' experiments on recognition memory (Chapter 7) capture this meaning. In behavioral ecology, *recognition* can refer to classifying objects or other animals appropriately on first encounter. For instance, *kin recognition* means treating relatives differently from other conspecifics, regardless of whether they have been encountered before. This corresponds to a second definition, "to know by means of some distinctive feature."

Kin recognition is discussed at the end of this chapter. First, however, we consider three examples of simple recognition learning: habituation, perceptual learning, and imprinting. In each case we ask two familiar questions: What are the conditions for learning? What is the content of learning, that is, what kind of representation underlies it? Habituation has been an important part of the "simple systems" approach to learning from its inception because it appears more amenable to neurobiological analysis than associative learning (R. F. Thompson and Spencer 1966; Papini 2008). Until relatively recently psychologists barely regarded habituation as genuine learning (J. D. Harris 1943), but we see in this chapter that animals are learning the characteristics of things in their world all the time, even when those things do not signal food, predators, sex, or other conventional reinforcers. Increased appreciation of this fact has led to new ways of testing nonverbal creatures for spatial, numerical, and social knowledge, as described in later chapters.

5.1 Habituation

When a frog's back is tickled, the frog reflexively wipes the spot that was tickled. If the same place is touched repeatedly, the wiping reflex becomes less and less vigorous. When a male white-throated sparrow hears the song of a neighbor on the edge of his territory, he approaches and flies back and forth, finally perching on a branch to sing a territorial song. Over the breeding season he becomes less aggressive toward familiar neighbors but still shows his aggressive display toward strangers and toward familiar neighbors in new places (Box 5.1). The waning of the frog's wiping reflex and

Box 5.1 Habituation, Association, and Individual Recognition

Males of many songbird species hold territories in the breeding season and exclude conspecific males from them (Collins 2004). Singing and aggressive interactions are prominent near territory boundaries, especially early in the breeding season. Birds that can learn who their neighbors are and focus time and energy on repelling new arrivals will have more time for other activities. As this functional notion suggests, birds do in fact respond less to familiar neighbors as the season advances. The learning involved includes both habituation and association (Falls 1982; Catchpole and Slater 1995). White-crowned sparrows habituate to the same song played repeatedly from the same location (Petrinovich and Patterson 1979). However, birds may also associate the songs of a particular singer with the place where he usually sings. For instance, white throated sparrows behave just as aggressively toward a neighbor's song played from a new location as toward a stranger's song played from that location (Figure B5.1; Falls and Brooks 1975). Male bullfrogs (*Rana catesbeiana*) behave similarly: aggressive responses habituate to repeated croaks from a single neighbor in a fixed location and dishabituate when a different frog calls from that location or the same frog calls in a new location. Bullfrogs discriminate between familiar and novel neighbors whether they call from the original or the novel location, apparently recognizing them as individuals (Bee and Gerhardt 2002).

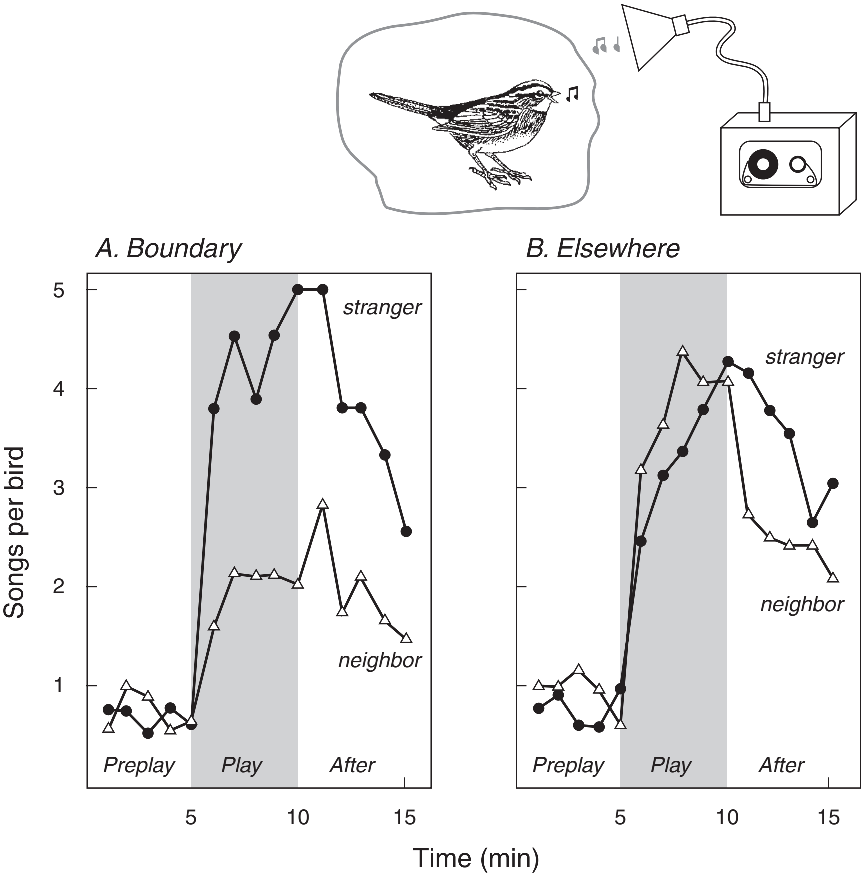


Figure B5.1. Response (songs per minute) of male white-throated sparrows to the recorded songs of neighbors or strangers presented either at the territorial boundary shared with the neighbor (A) or elsewhere in the subject bird's territory. Data from Falls and Brooks (1975), redrawn with permission.

Males of some bird species have repertoires of up to hundreds of different songs, which may function partly to prevent females habituating to them (Catchpole and Slater 1995; Collins 2004). If neighbor-stranger discrimination depends on associating the neighbor's songs with the direction from which they are usually heard, neighbor-stranger discrimination might be less sharp in species with large repertoires, but this is not always so. Songs within an individual's repertoire may have some shared characteristics, permitting generalization among them. Such individual differences have been documented in great tits in both the field and operant tests in the laboratory, where birds trained to discriminate between the songs of different males generalize to unfamiliar songs of the same individuals (Weary and Krebs 1992; but see Searcy, Coffman, and Raikow 1994).

The ability to identify a particular individual by any of several distinctive features presumably develops through associating those features, as in examples of perceptual learning in the main text. For example, a male hamster habituated to the vaginal scent of a familiar female (see Figure 3.4) also proves to be habituated to her flank gland scent (Johnston and Bullock 2001; for a similar effect in ground squirrels see Mateo 2006). Males that have never met the stimulus female do not transfer habituation between scents, showing that habituation does not simply generalize from one scent to the other. To transfer between two of a female's odors a male needs to interact with her, even if through a screen. Contact with the female's body while she is anesthetized also suffices, perhaps because warmth, touch, or some other chemicals from the female potentiate associations among her odors. This mechanism would mitigate against associating odors that occur together by chance, as when two different individuals have passed by the same place (Johnston and Peng 2008).

Cross-modal associations, as between faces and voices, may also play a role in individual and species recognition. Some birds seem to associate the song of another species with its appearance (Matyjasiak 2004; D. Grant and Grant 2008). When rhesus macaques trained to discriminate among colony mates in photos were played the vocalizations of those animals, an individual's voice seemed to access the same representation as the pictures (Adachi and Hampton 2008). In Chapter 12 we will see that social primates acquire elaborate networks of associations among the characteristics of social companions.

the waning of the sparrow's aggressive display have both been studied as examples of habituation even though the behaviors differ greatly in complexity and wane over different time courses. In both cases behavior changes in such a way that time and energy are not wasted in unnecessary or inappropriate behavior.

Habituation is a widespread form of behavioral plasticity, found even in one-celled organisms and in many behavior systems (W. Thorpe 1956; Papini 2008). It also appears to be the simplest: exposure to a single event is certainly the most elementary of experiences. However, this apparently elementary experience can have some quite complex effects, both long-term and short-term. Responses may increase or decrease in intensity when they are repeatedly elicited, and sometimes a single response does first one and then the other. Moreover, exposure to a single event can produce perceptual learning, latent inhibition, and/or imprinting. This section is organized around the same topics as Chapter 4. We look first at the conditions for habituation learning, its contents, and the effects of learning on behavior and then consider three theories about the content of learning in habituation.

5.1.1 Conditions for learning

Habituation is identified operationally as a decrease in responding resulting from repeated stimulation. (Confusingly, the procedure involved is also called *habituation.*) The response measured can be anything from a simple reflex to behavior of a whole animal. However, changes in behavior due to fatigue of receptors or effectors

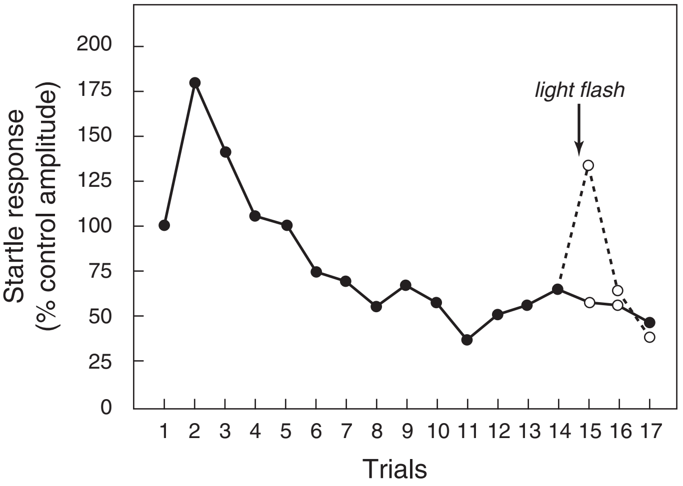


Figure 5.1. Habituation and dishabituation of rats' startle response to a sudden sound. Rats whose data are represented by the dotted line received a flash of light just before the fifteenth sound. Redrawn from Groves and Thompson (1970) with permission.

are not accepted as habituation. Fatigue can be eliminated as the cause of decreased responding by demonstrating *dishabituation:* a novel stimulus restores responding to the original habituating stimulus. Figure 5.1 shows an example from rats in which presentation of a light restored the startle response to a sound. (Startle is a primitive defensive response to sudden strong and therefore potentially dangerous stimuli. In mammals, the whole body reacts as the animal instantly tenses its muscles and draws its head and limbs close to its body. The reaction is conveniently measured by placing the animal in a motion-sensitive cage.)

Experience with a single event is described by the answers to a few simple questions: What is it? How long and intense is it? How often does it occur? How many times has it occurred? What was the animal's age and motivational state during exposure? These same questions define the key parameters of other forms of recognition learning.

Stimulus quality

Specificity is one of the defining features of habituation. Completely general response decrement would be attributed to receptor adaptation or response fatigue. However, habituation does generalize to stimuli similar to the habituating stimulus. Taking the stimulus-specificity of habituation as a given implies that in dishabituation the animal is classifying the new stimulus as different from the old one. Because the behaviors that habituate do not have to be trained initially, this so-called *habituation-dishabituation paradigm* is a powerful tool for studying basic memory and classification processes in nonverbal organisms, including human infants. The data on hamsters' odor discrimination in Figure 3.4 is one example. A large body of literature on infants' cognition rests on the fact that babies orient toward novel visual and auditory stimuli. Orienting (looking and/or modifying sucking rate) habituates to repeated stimuli but is shown at a higher level when a novel stimulus appears. Thus for example, a baby hears "ba . . . ba . . . ba" and then "pa . . . pa" to test if she discriminates between speech sounds. Similar tests have been used with monkeys and rats to study spatial, numerical, and social discriminations (Chapters 8, 10, 12, and 14). Notice, however, that stronger responding to a novel stimulus than to the original habituating stimulus is not the same as the enhancement (i.e., dishabituation) of responding to the *original* stimulus illustrated in Figure 5.1. Strictly speaking then, the popular habituation-dishabituation test should be called something like the habituation-discrimination test.

Number of stimulations

It almost goes without saying that the more an eliciting stimulus is presented, the more the response decreases. In a classic article, R. F. Thompson and Spencer (1966) claimed that responding was a negative exponential function of number of stimulations. This suggests that, like associative learning, the learning in habituation reduces the discrepancy between "expected" and actual events in a manner proportional to the discrepancy. However, the exact form of habituation curves depends on how responding is measured (Hinde 1970b; Figure 5.2). Unlike theories of associative learning, theories of habituation have not always differentiated the underlying learning, the theoretical habituation process, from performance of the habituated response. However, the phenomenon of *habituation below zero* (R. F. Thompson and Spencer 1966; Hinde 1970b) suggests that a learning-performance distinction may be needed for habituation, too. Continuing stimulation after responding stops results in slower recovery than simply habituating to zero, suggesting that learning continues in the absence of measurable responding.

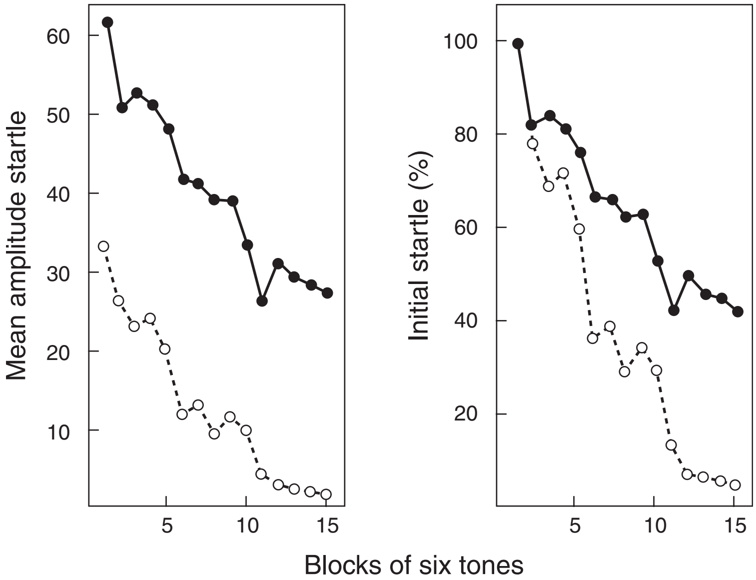


Figure 5.2. How choice of absolute (left) or relative response measures can influence the pattern of data, illustrated with effects of amphetamine on habituation of startle in rats. The panel on the left suggests that the drug (filled circles) raises the level of responsiveness without affecting the rate of habituation, whereas that on the right suggests that the drug slows habituation. Redrawn from Davis and File (1984) with permission.

Increasing numbers of presentations also reduce generalization to similar stimuli. For example, Gillette and Bellingham (1982, cited in Hall 1991) habituated rats to drinking a novel fluid flavored with salt (NA) and sucrose (S). The rats drank little of this novel fluid at first but gradually increased their consumption. Generalization was measured by the rats' willingness to drink NA or S alone. The rats drank *less* NA or S the more they had been habituated to the mixture. That is, the more they had been exposed to NA+S the better they discriminated this compound from its elements. This is just the opposite of what would be expected if the compound was simply the sum of elements and indicates that exposure results in learning about the stimulus, that is, perceptual learning (Hall 1991).

Timing and intensity

Responding typically declines faster during massed than during spaced presentations of the eliciting stimulus. But as discussed in Chapter 4, such an observation is not enough to infer differences in learning. Differences in learning at T1 (i.e., during the train of stimuli) must be assessed by a common test at a later time, T2. Here, the more profound decline has been seen after spaced training (Figure 5.3; M. Davis 1970). The same idea applies to the effects of stimulus intensity (M. Davis and Wagner 1969). R. F. Thompson and Spencer (1966) claimed that habituation is "more rapid and/or pronounced" with weaker stimuli. But when responding is measured in a standard test after exposure to different schedules and intensities of stimulation, the results can be surprising. For instance, a relatively loud tone evokes a smaller startle response in rats habituated with a

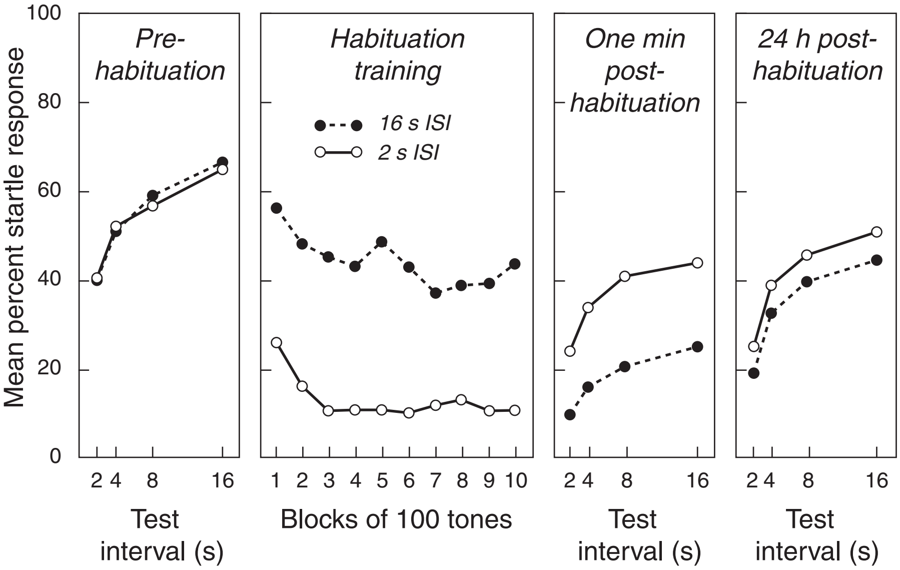


Figure 5.3. The importance of giving a standard test after different habituation experiences. Two groups of rats were pretested (left panel) and then habituated to tones presented with an interstimulus interval (ISI) of either 2 or 16 seconds and tested 1 minute or 24 hours later at a variety of ISIs (M. Davis 1970). Note how leftmost and rightmost panels depict the same test before and after the habituation experience. Redrawn with permission.

series of tones of gradually increasing loudness than in rats exposed to an equal number of tones of the same loudness as the test tone (M. Davis and Wagner 1969).

The interval between T1 and T2

W. Thorpe (1956) stipulated that only a "relatively permanent" response decrement counts as habituation. In fact, however, repeated stimulation can have two distinct effects, one short-term and one lasting for days or weeks (Staddon and Higa 1996). Even simple response systems such as gill withdrawal in *Aplysia* show long-term retention of habituation (Figure 5.4). However, long-term habituation is also gradually forgotten, and generalization gradients broaden as time passes, as if the animal forgets details of the habituating stimulus (Hall 1991).

State variables: Sensitization

Repeated stimulation can increase responding as well as decreasing it, especially if the stimulus is moderately aversive. In the experiment shown in Figure 5.1, the rats were actually more startled by the second and third tones than by the first one, although startle later declined. This biphasic curve is typical of the results of many experiments

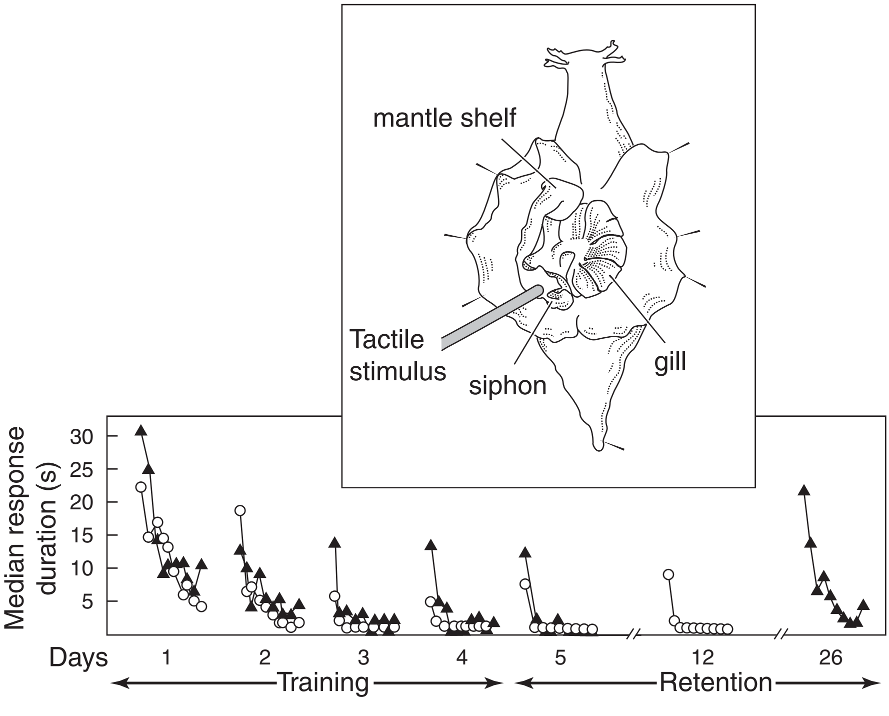


Figure 5.4. Long-term and short-term habituation of *Aplysia's* siphon withdrawal to a jet of water applied to the siphon (tactile stimulus). No trials were administered between the last training day and the tests on Day 5 and Day 12 (group represented by open circles) or Day 26, yet habituation was retained. At the same time, habituation developed within each day. Redrawn from Carew, Pinsker, and Kandel (1972) with permission.

on habituation. The initial increase seems to reflect an independent process of *sensitization,* a general enhancement of responsiveness to a whole class of stimuli, not just the one being habituated. Sensitization often has a shorter time course than habituation, as in Figure 5.1.

The sensitizing effect of moderately strong stimuli may be responsible for some instances of "dishabituation." Functionally, it seems as if a potentially dangerous stimulus alerts the animal, making it more responsive to whatever comes next. Associative potentiation of the rat's startle response (Davis et al. 1993) fits this description: rats startle more when they are in the presence of a signal associated with shock. However, dishabituation can reflect a separate process from sensitization. Siphon withdrawal in the sea slug *Aplysia* wanes when the siphon is repeatedly squirted with a jet of water (Figure 5.4). If the animal's tail is touched or shocked, siphon withdrawal is enhanced in both habituated and untrained animals. In an elegant series of experiments, Marcus, Nolen, Rankin, and Carew (1988) showed that sensitization and dishabituation can be dissociated in Aplysia in three independent ways, thus lending support to a two-process theory of habituation (Groves and Thompson 1970). For instance, the best dishabituating stimulus is a touch to the tail or a relatively weak shock, whereas strong shocks or many shocks to the tail are the best sensitizing stimuli. Sensitization of this response in *Aplysia* has been the subject of a rare study of the phylogeny of learning at the neural level (see Papini 2002).

5.1.2 Diversity of effects on behavior

Examples of habituation like startle in the rat or the wiping reflex in frogs seem to involve little more than changes in specific reflex circuits. But complex behaviors of whole animals like the territorial behavior of birds described in Box 5.1 also habituate. As another example, rats or hamsters released into a large open enclosure (an "open field") approach and sniff objects in it, exploring them. Exploration wanes over time, but if some of the objects are moved to new places, the animals explore them again. Renewed exploration specific to the relocated objects shows that their original locations were learned. As another example, when wild vervet monkeys hear the call of a member of their troop broadcast from a loudspeaker, they gradually stop looking toward the hidden speaker. Habituation transfers to acoustically dissimilar calls with the same referent (e.g., both are given when another group of vervets is approaching). It seems the animal is not habituating to the physical stimulus so much as to the reception of a certain kind of information (see Chapter 14).

5.1.3. Contents of learning: Three models

Over 60 years ago, one of the first reviews of habituation concluded, "It will be obvious, . . . that no 'mechanism' of habituation will be found. There are quite probably several mechanisms . . . any single explanatory principle would have to be too general to be satisfactory" (J. D. Harris 1943, 388). This conclusion is just as apt today. In this section we consider three models of habituation. The two classic ones differ in that one is a simple model of changes in S-R connections, and the other assumes incoming stimuli are compared to a more complex representation. The third, more recent, model depicts habituation as a form of associative learning (for further discussion see Hall 1991; Macphail 1993).

Sherrington's reflex model

The simplest model of habituation dates from Sir Charles Sherrington's studies of animals with severed spinal cords in the late nineteenth century. Because this surgery removes influences from the brain, habituation in spinal animals necessarily reflects changes in specific reflex pathways, S-R connections. As in S-R accounts of associative learning, this model does not distinguish between learning and performance: learning, the decrement in connection strength, is directly reflected in decreased responding. As a general account of habituation this is simply a restatement of behavioral observations in neural terms and as such is relatively impoverished. It does not predict any new phenomena or specify the precise form of the decrement in connection strength. However, this model can be elaborated in several ways to account for phenomena such as dishabituation and sensitization (e.g., Horn 1967; Davis and File 1984). It is a reasonable account of some examples of habituation such as siphon withdrawal in *Aplysia*. Nevertheless, a simple S-R account is not very useful for understanding habituation of more complex behaviors or possible changes in the representation of stimuli during habituation.

Sokolov's neuronal model

A more complex model couched in neural terms is Sokolov's (1963) comparator model. Here learning consists of building up a representation of the features of a stimulus, the *neuronal model*. How this takes place is not specified but it could involve the kind of within-event learning discussed in Section 5.2. Incoming stimuli are compared to existing neuronal models before being acted on. If there is a match, the initial response to the stimulus is inhibited, that is, behavioral habituation is observed. If the incoming stimulus is discrepant from the neuronal model, an *orienting response* (OR) occurs and the neuronal model is modified to reduce its discrepancy from the incoming stimulus. This scheme therefore distinguishes between learning (modification of the neuronal model) and performance (the OR based on detection of a discrepancy).

Some examples of habituation seem to require such a comparator account. One is the *missing stimulus effect* (Sokolov 1963). If an animal is habituated to stimuli coming at regular intervals and then one stimulus is omitted, the habituated response reappears at the time the omitted stimulus was due. Similarly, hamsters that have learned the locations of objects through exploration spend extra time in the location from which a familiar object has just been removed (Poucet et al. 1986). The simple reflex model has trouble with such effects because the absence of a stimulus has significance only by comparison to expected input (but see Hall 1991). However, the comparator model also has its troubles. In particular, an increasing series of stimulus intensities should not result in greater response decrement than a series of presentations of the same intense stimulus (Davis and Wagner 1969; Groves and Thompson 1970). The neuronal model should match the test stimulus better when that stimulus has been presented all along than when different stimuli have been presented.

Sokolov proposed a specific neural embodiment of his model: the neuronal model is built up in the cortex, and it inhibits activity in the reticular formation, but this system cannot apply to habituation in spinal animals or in *Aplysia*. There may be different neural mechanisms for behavioral habituation in different systems. For potential generality there is a lot to be said for more abstract "black box" models like the one discussed next.

Wagner's SOP model

Accounting for an apparently simple kind of learning in terms of a more complex one may seem unappealing, a violation of Lloyd Morgan's Canon. Yet one influential model of habituation does just that: in this model, habituation results from associating the habituating stimulus with the context in which it appears (Wagner 1978, 1981). This account integrates habituation with associative learning and with standard features of short-term memory. (Hence its acronym, *SOP,* for *standard operating procedure* of memory.) In the SOP model (Figure 5.5) incoming stimuli are compared to the contents of active or *working memory*. Working memory has two levels or states. The highest level of activation, A1, corresponds to the focus of attention or "rehearsal." The contents of A1 are directly read out in behavior appropriate to the stimulus being processed. If stimuli from food are in A1 the animal will be engaged in food-related activities; if a sudden loud noise is being processed, the animal will startle. Behavior appropriate to incoming stimuli will be observed whenever the incoming stimulus is not already represented in one of the levels of active memory (A1 or A2).

Representations (nodes) in A1 fade into the A2 state, corresponding to representation in working memory just outside the immediate focus of attention, and thence into long term or inactive memory (I). The behavioral readout of A2 is therefore behavior appropriate to the memory of a very recent event. Representations can also be activated into A2 associatively, that is, the animal can be reminded of them. The distinction between the two states of active memory captures the notion that remembering something and experiencing it are not the same and may evoke correspondingly different behaviors. If an event is already represented in A2, this will interfere with its ability to be evoked into A1. In this way, expected events (associatively activated into A2) evoke a smaller response than unexpected ones. Short-term memory has limited capacity so that new, unexpected, stimuli displace stimuli currently

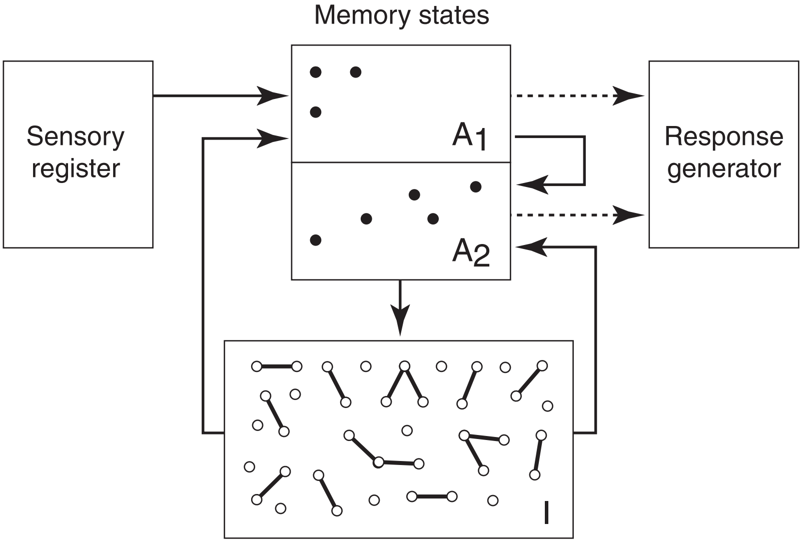


Figure 5.5. Wagner's SOP model of habituation as depicted by Roitblat (1987), indicating memory nodes (circles) and associative links (lines). Redrawn with permission.

being processed or *rehearsed* in A1. Associative learning occurs only when the stimuli to be associated are processed simultaneously in A1. On this view associatively activated representations (represented only in A2) should not be able to function as USs, contrary to the evidence about US images in Chapter 4. Short-term habituation occurs because the more recently a stimulus has been primed into A1 the more it occupies A1 and/or A2. This limits the ability of new occurrences of that stimulus to command processing in A1 and evoke behavior. Long-term habituation reflects association of the habituating stimulus with its context. Thus this model differs from the other two in distinguishing between long-term and short-term habituation.

The SOP model generates a number of novel predictions which have inspired clever tests. For example, habituation should be retarded by presenting "distractors" between occurrences of the target stimulus in a sort of dishabituation paradigm. Whitlow (1975) did this by presenting tones to rabbits and measuring vasoconstriction in the ear (essentially the extent to which the rabbits "pricked up their ears" to the sounds). He presented tones at various intervals to test the prediction that responding is evoked if incoming stimulation does not correspond to the representation currently active in short-term memory. When the same tone was presented twice in succession, the response to the second tone was reduced at intertone intervals up to 150 seconds. However, if two successive tones differed, the response to them was the same, even when the intertone interval was as little as 30 seconds. The stimulus-specific response decrement could be eliminated by presenting a distractor—flashing a light and touching the rabbit—between successive presentations of the target stimulus (see Figure 7.10).

In Wagner's model, the animal becomes less responsive to the target because it learns to expect it in the experimental context (i.e., the representation is associatively evoked into A2 by the context). Thus habituation should be context-specific. Furthermore, it should be possible to "extinguish" habituation by exposing the animal to the context in the absence of the habituating stimulus. Latent inhibition reflects the same mechanism as habituation in this model because if a stimulus is not well represented in A1 it is less available to be associated with another stimulus. Tests of the prediction that both latent inhibition and habituation should be specific to their original training context have had mixed results (McLaren and Mackintosh 2000; Hall 2003). For example, latent inhibition generally fails to transfer to new but familiar contexts, whereas habituation does transfer. Functionally, whether or not habituation transfers should perhaps depend on the animal and the context. For instance, contact with the body of another animal is innocuous as long as you are in a herd or a communal burrow, but it's potentially dangerous when you are alone.

In conclusion, the SOP model is appealing because it applies to a broader range of phenomena than the earlier simpler models. It allows for complex behavior and for short-term as well as long-term habituation, and it has links with standard memory models and associative learning theory. In the years since it was first proposed it has been elaborated to encompass a wider variety of phenomena from conditioning by allowing both CSs and USs to have multiple components in the style of the models discussed in the next section (see Brandon, Vogel, and Wagner 2003).

5.2 Perceptual learning

Perceptual learning refers to learning the characteristics of stimuli as distinct from learning their relationship to other stimuli. The classic demonstration of perceptual learning is an experiment by E. Gibson and Walk (1956). Young rats were exposed to large triangles and circles on the walls of their home cages until they were 90 days old. Then they were trained to approach one of these patterns and avoid the other. Rats familiar with the stimuli learned the discrimination much faster than rats for which the stimuli were novel. This finding seems opposite to what would be expected if exposure to the shapes produced latent inhibition. A way to understand it is to realize that learning depends on both *discriminability* and *associability* of stimuli. Associability corresponds to α or salience in the Rescorla-Wagner model (Chapter 4). Exposure to a stimulus may reduce its associability with reward and at the same time enhance its discriminability from similar stimuli, as shown by the following experiment (Hall and Honey 1989).

Rats were exposed to a horizontally and a vertically striped plaque in a runway or their home cages. Then they had a go/no go discrimination in the runway with one of the plaques as the reinforced stimulus (i.e., they were rewarded for running when the designated plaque was at the end of the runway but not when it was absent). The preexposed rats learned the discrimination more slowly than a control group that had been preexposed only to the runway (Figure 5.6). This illustrates latent inhibition (Section 4.4.6): preexposure slowed associating the familiar plaque with reward. After learning the presence-absence discrimination with one of the striped plaques, the rats were tested in the runway with the other one. The control rats generalized their relatively fast running to the second plaque, which they had not seen before. The preexposed groups generalized less, that is, they discriminated better between the patterns. In more recent experiments, such effects have been explored using liquids made up of different

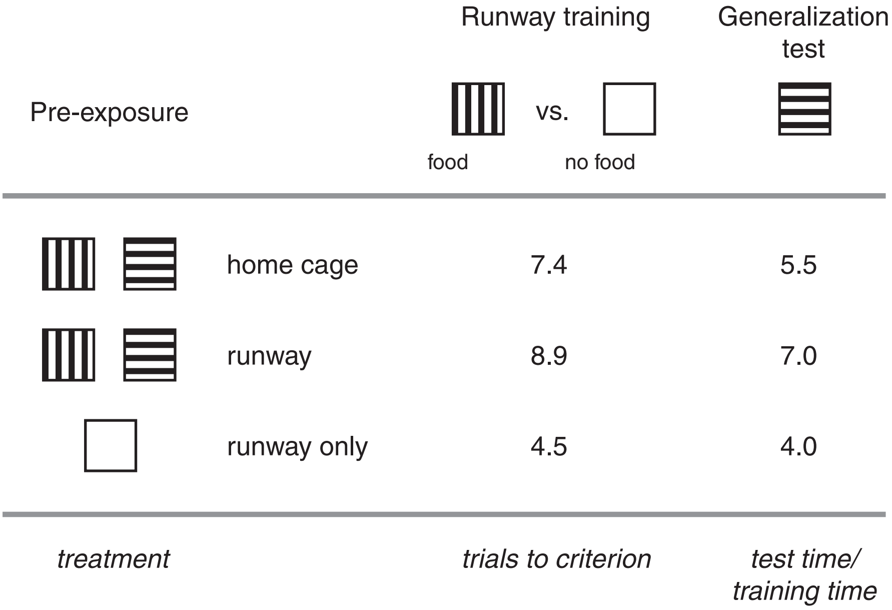


Figure 5.6. Procedure and results of Hall and Honey's (1989) demonstration that preexposure both reduces associability and enhances discriminability. Faster discrimination learning is indicated by fewer trials to criterion. In the generalization test, the striped plaque not used for training was presented in extinction and its effects measured as the ratio of running times to running time at the end of training; hence, the higher the ratio the less the generalization, that is, the rats ran more slowly to the test plaque than to the reinforced plaque.

components. For instance, two flavored solutions such as saline and sucrose may be made more similar by adding a third flavor such as lemon to both of them (McLaren and Mackintosh 2000).

5.2.1 A model of stimulus representation

William James (1890, 511) described what seems to go on during perceptual learning as follows:

> How does one learn to distinguish claret from burgundy? . . . When we first drank claret we heard it called by that name, we were eating such and such a dinner, etc. Next time we drink it, a dim reminder of all those things chimes through us as we get the taste of the wine. When we try burgundy our first impression is that it is a kind of claret; but something falls short of full identification, and presently we hear it called burgundy. During the next few experiences, the discrimination may still be uncertain—"which," we ask ourselves, "of the two wines is this present specimen?" But at last the claret-flavor recalls pretty distinctly its own name, "claret," "that wine I drank at So-and-so's table" etc.; and the name burgundy recalls the name burgundy and someone else's table . . . After a while . . . the adhesion of each wine with its own *name* becomes . . . inveterate, and . . . each flavor suggests instantly and certainly its own name and nothing else. The names differ far more than the flavors, and help to stretch the latter further apart.

James's idea—that things initially difficult to discriminate become more discriminable by means of associations among their unique features—is captured in a general model of stimulus representation proposed by McLaren, Kaye, and Mackintosh (1989; McLaren and Mackintosh 2000). The model starts from the assumption (Estes 1950) that stimuli are composed of a number of discrete elements. In James's example, the elements of each wine include its name, its flavor, and the occasions on which it was drunk. Elements are assumed to be sampled randomly each time the stimulus is encountered (Figure 5.7a). In earlier versions of stimulus sampling theory

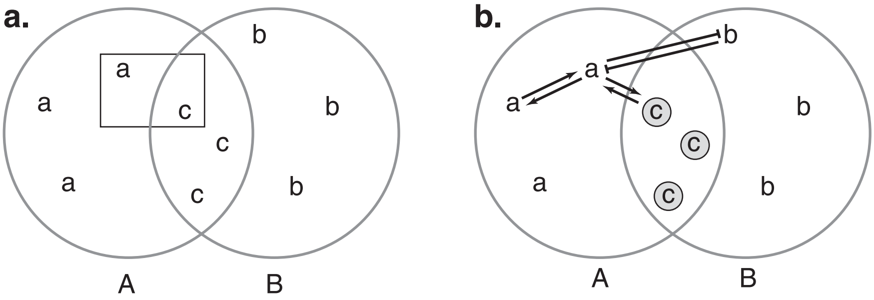


Figure 5.7. The model of perceptual learning proposed by McLaren, Kaye, and Mackintosh (1989). a: Circles represent two stimuli, A and B, that have some common elements (c's) as well as unique ones (a's and b's). A subset of elements (inside the rectangle) is sampled when A appears. b: The situation that develops after exposure to A and B, with reference to representative elements. Each a element develops excitatory associative links with other a elements and with the common elements, c. Inhibitory links develop between a and b elements. Meanwhile, the most frequently encountered elements, the c's, acquire the most latent inhibition (gray circles). After McLaren, Kaye, and Mackintosh (1989) with permission.

(e.g., Estes 1950; Pearce 1987) each stimulus element is a little CS independently associated with the US. But this approach becomes much more interesting and powerful if elements also become associated with each other as suggested by James. Each stimulus element activates a unit or node in a hypothetical network of such nodes (Hall 2002). When a stimulus is presented the nodes corresponding to stimulus elements being sampled are activated both externally, by the element itself, and internally, through associatively modifiable links with other nodes. Learning reduces the discrepancy between internal and external inputs to a node by strengthening connections among the nodes most often activated together, that is, those corresponding to features of the same stimulus. As a result, eventually a subset of elements will tend to activate nodes corresponding to the whole set (Figure 5.7b). The taste of claret will immediately remind one of the name, the occasions on which it was drunk, and so on. In effect, the network of associated nodes is a neuronal model of the stimulus.

This Jamesian account indicates how stimuli become "unitized," but to explain how at the same time wines that share features might become more discriminable from one another, McLaren et al.'s explanation calls upon latent inhibition. Exposure to stimuli with common elements will give most latent inhibition to their common elements, since by definition those elements appear most often. Then when one of these familiar stimuli is to be associated with a US, strongest associations will develop to the unique elements. In addition, sets of nodes corresponding to elements unique to the different stimuli will develop inhibitory connections with each other, as indicated in Figure 5.7b. In James's example, burgundy reminds the inexperienced taster of claret, that is, claret elements are activated internally. Inhibition develops between elements unique to burgundy and those unique to claret because the expectation of "claret" is not activated externally when burgundy is presented. At the same time elements common to the two wines such as a red color will undergo latent inhibition. These ideas suggest that perceptual learning will be more evident relative to latent inhibition with stimuli that are initially less discriminable, that is, have more common elements. The relevant data are consistent with this prediction (McLaren and Mackintosh 2000; Hall 2003).

5.2.2. Within event learning

The model just reviewed hinges on the assumption that separable features of a single event are associated with each other just as CSs are associated with USs. There is considerable evidence for this assumption from experiments on *within event learning*. The logic of such experiments is to create events with separable elements, expose animals to this compound, then give one element a new significance and measure behavior to the other. An experiment on within event learning is thus much like a sensory preconditioning experiment (Figure 4.7) except that the stimuli to be associated occur simultaneously. If the animal views them as features of the same event, then its behavior to one element should reflect conditioning with the other (Rescorla and Durlach 1981).

For example, rats might first drink two compound flavors such as sweet+sour and salty+bitter. In the second phase of the experiment, an element of one compound—say sweet—is paired with poison, and as a control a single element of the other compound—say salt—is presented alone. In the final phase, when the rats choose between the two elements not encountered in the second phase (i.e., sour vs. bitter), they prefer to drink the flavor not paired with the poisoned one, that is, bitter. Parallel results have been obtained using lights and tones for rats and visual stimuli for pigeons (Rescorla and Durlach 1981). Such within event learning increases rapidly and monotonically with number of exposures to the compound. Learning about simultaneous events can even be superior to learning about successive events (see Rescorla and Durlach 1981). And, as one would expect, within-event learning can be extinguished by presenting one or the other element of the event by itself. However, although retraining after extinction is normally quicker than original acquisition with Pavlovian or instrumental conditioning (the phenomenon of *savings*), retraining of within event learning is difficult or impossible after extinction. This finding is consistent with the view that animals originally treat the compound stimulus as a single unanalyzed unit or configuration. On this view (Pearce 1994b) the acquired value of one element transfers to the other through generalization because the individual elements are similar to their compound. Exposure to the elements in isolation sets up representations of these as separate events, and associative changes, involving them are no longer related back to the compound.

Although other processes may sometimes be involved in perceptual learning, this model shows that within-event associations can effectively account for much of what is known about how animals form representations of the events and objects they are simply exposed to (McLaren and Mackintosh 2000; Hall 2003). This same learning process is likely involved in coming to recognize individuals through multiple distinctive cues, as discussed in Box 5.1. In Chapter 6 we will see that it may also be involved in explicit discrimination and category learning.

5.3 Imprinting

Precocial birds like chickens, ducks, and geese can run around within a few hours after hatching. In natural conditions they are kept from running away from their mother at this time, when they still need her for warmth and protection, by rapidly developing a preference for following her rather than other large moving objects. In experiments, they have become attached to moving balls, dangling sponges, flashing lights, stuffed ferrets, and many other objects instead, through the learning process known as *imprinting*. Although it had been described by Douglas Spalding in the 1870s, Konrad Lorenz's (1935/1970) discussion of imprinting was responsible for an outpouring of research on it in the 1950s and 1960s (see Bateson 1966). Lorenz described how birds that had been removed from others of their own species early in life would court and try to mate with members of the species that had raised them, including Lorenz himself. Lorenz claimed that the process responsible for acquisition of such social preferences was a kind of learning distinct from "ordinary learning," by which he meant Pavlovian or operant conditioning (Lorenz 1970, 377). He based this claim on four apparently special characteristics. *(1)* Imprinting could occur only during a *critical period,* early in life. *(2)* After this, it was irreversible. *(3)* Imprinting influences behavior that is not, and often cannot be, shown at the time of learning, that is, adult sexual behavior. *(4)* From experience with a particular individual, normally the mother, the animal learns characteristics of its species.

It soon became apparent (cf. Bateson 1966; Bolhuis 1991) that Lorenz's description of a gosling instantaneously and irreversibly imprinted with a lifelong preference for people after one brief glimpse is far too simple. The phrase *critical period* was replaced by *sensitive period* or *sensitive phase,* implying that the onset and offset of sensitivity were gradual. And, as Lorenz (1935/1970) had acknowledged, the nature of the imprinting stimulus was important. Rather than being irreversible, early preference for an inadequate artificial stimulus could sometimes be replaced by preference for a more naturalistic one. And the differences between imprinting and "ordinary learning" turned out to be not so great after all.

Imprinting was depicted as a "special," "preprogrammed" kind of learning because it is shown only by certain species at certain times in their lives (e.g., Staddon 1983). But it is actually no more "preprogrammed" than any other kind of learning, and it shares many properties with other examples of recognition learning. Most of this section is about *filial imprinting,* acquisition of social preferences in young birds, because most work has been done in this area. Formation of sexual preferences (Section 5.3.2) may involve some different processes.

5.3.1 Conditions and contents of learning

Laboratory tests of imprinting

When a chick or duckling is exposed to an effective imprinting object, it spends more and more time close to it, twittering softly and snuggling up to it. It spends less and less time shrilly peeping ("distress calling") and trying to escape. Demonstrating that such changes are due to experience with the object rather than simply maturation requires two potential imprinting stimuli, A and B. Some animals are exposed to A in the imprinting situation and some to B. Then all animals are given a choice between A and B. For example, Bateson and Jaekel (1976) placed chicks in a running wheel facing a red or a yellow flashing light. The chicks could run toward the light but they did not get any closer to it. After varying amounts of experience with one of the lights, the chicks were tested in another running wheel on a track with the red light at one end and the yellow light at the other (Figure 5.8). When the chick ran toward one light it was transported toward the other, but it could continue to run toward its preferred light even when carried to the opposite end of the track by its efforts. Preference was measured as proportion of all wheel revolutions in a particular direction. Other tests of imprinting take advantage of the fact that a bird will learn an instrumental response to see an object on which it has been imprinted (e.g., Hoffman 1978; Figure 5.9). Such an object also suppresses distress calling when it appears.

Length of exposure

Notice that when birds are trained in a running wheel as in Figure 5.8, running is not instrumentally reinforced because they never get any closer to the imprinting object. Thus sheer exposure to an object is sufficient for a preference to develop. In fact, if exposed to them for long enough, chicks imprint to patterns on the walls of their pens (see P. Bateson 1966). Just as with any other learning phenomenon, length of exposure, type of stimulus, and the state of the animal must all be considered together. A few minutes' exposure to a conspicuous moving object during the first day or two after hatching may have effects only matched by an inconspicuous stationary object after many days' exposure (ten Cate 1989). The effects of length of exposure may depend on the species. Lorenz (1935/1970) described two extremes of imprintability. A greylag gosling that had once seen people would never afterward associate with geese, but curlews would always flee

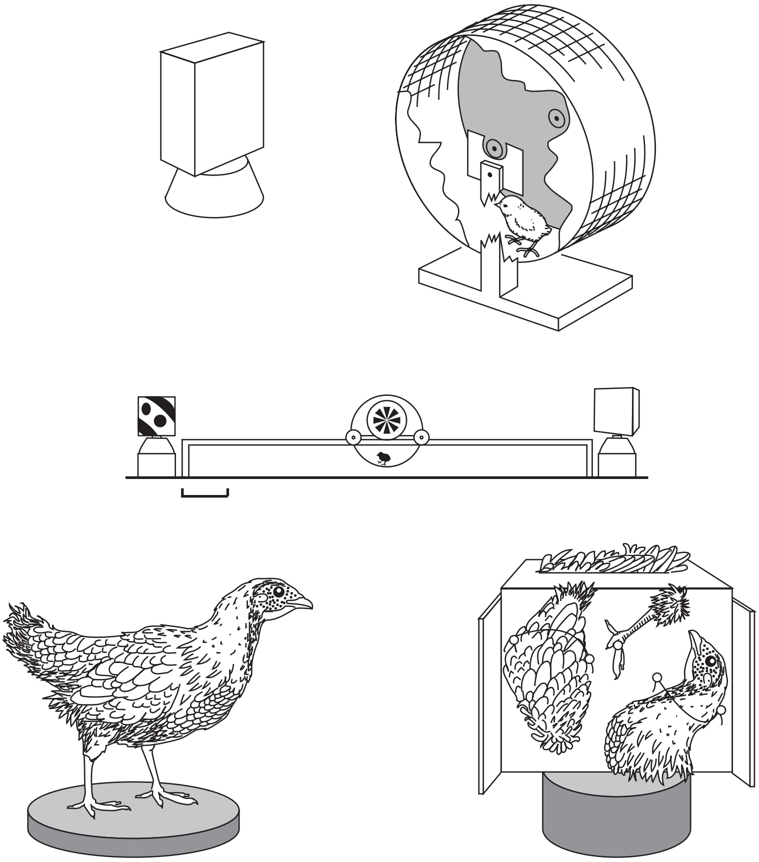


Figure 5.8. Running wheels for imprinting chicks (top row) and testing their preferences (middle), and some of the stimuli used by Bateson, Horn, and their colleagues. Redrawn from Horn (1985) and Bateson and Wainwright (1972) with permission.

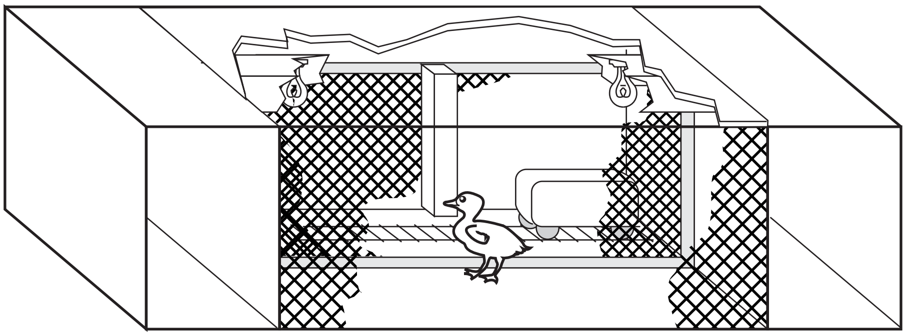


Figure 5.9. Apparatus used for imprinting ducklings and testing instrumental responding reinforced by presentation of the imprinting stimulus. The ducking pecks the square pole in the middle of his compartment to illuminate the compartment in which the imprinting object moves back and forth. Redrawn from Eiserer and Hoffman (1973) with permission.

from people no matter how much they had been exposed to them. Yet Lorenz's assertion that imprinting is instantaneous and irreversible has nearly always been tested on species other than greylag geese, such as domestic chicks and ducklings (see Goth and Hauber 2004).

Type of stimulus

Lorenz (1935/1970) claimed that adults of the bird's own species were more effective imprinting objects than artificial stimuli. Species-specific stimuli do seem to be special for both domestic chicks and ducklings, but not exactly in the way one might expect. Domestic chicks prefer stuffed hens of the junglefowl (their wild ancestors; see Figure 5.8). A preference for fowllike objects develops in the first 2 to 3 days of life as a result of certain nonspecific experiences. It sums with learned preferences. Rearranged stuffed junglefowl (Figure 5.8), stuffed ducks, or even ferrets (a potential predator) are approached as much as junglefowl, perhaps because they have eyes (Johnson and Horn 1988; Bolhuis 1996). These findings indicate that in natural conditions imprinting to the mother is supported, or canalized, by preferences for species-specific stimuli which ensure that the young bird is initially attracted to the mother rather than to other moving objects (see ten Cate 1994). The role of filial imprinting may be to establish not species identification, as suggested by Lorenz, but identification of a particular individual—the mother—within that species (Bateson 1979).

The sensitive period

Many aspects of behavioral development have a sensitive period, a time when they are most susceptible to environmental influence (see Hogan and Bolhuis 2005). Filial imprinting needs to take place only at the beginning of life because its immediate function is to keep the young bird with its mother at this vulnerable time. Accordingly, filial imprinting in chicks and ducklings takes place most readily between a few hours and a few days after hatching. By itself, however, a sensitive period does not make imprinting qualitatively different from associative learning: how learning depends on age is a different question from what kind of experience causes it. Intuitively, the sensitive period reflects a developmental timetable in which imprintability develops at a certain point in ontogeny and further maturational processes end it. This *clock model* (ten Cate 1989) probably accounts for the onset of the sensitive period, but it does not explain its end.

On the alternative account, variously called the *competitive exclusion* (Bateson 1981; 1987), *capacity* (Boakes and Panter 1985), or *self-termination model* (ten Cate 1989), imprinting is fundamentally different from most other forms of learning because once an animal is fully imprinted to one object it cannot become imprinted to any other object. That is, imprinting as intrinsically self-terminating (Bateson 1990), as if there were a fixed number of neural connections that it could occupy. Once these have been used up the animal may still learn to recognize other stimuli such as food or siblings, but these do not, in Bateson's terms, "gain access to the executive system" for filial behavior. This model thus distinguishes between S-S learning—learning the characteristics of the imprinting object—and S-R learning—connecting the features of the object to the filial behavior system.

Is imprinting a kind of conditioning?

The observation that conspicuous moving or flashing objects lead to faster imprinting than stationary ones suggests that imprinting is a form of Pavlovian conditioning in which the static features of the object function as the CS and visual motion as the US. This suggestion leads to a number of testable predictions that contrast with those of the most explicit alternative, namely, that imprinting is a form of perceptual learning in which the animal simply learns the features of the imprinting object and approaches it because it is familiar (see van Kampen 1996). On the perceptual learning view, moving objects are effective because they are more conspicuous than stationary objects. Once the conspicuous features of the mother have acquired value through exposure in the sensitive period her inconspicuous features can go on being learned about. As this discussion suggests, the phenomena of perceptual learning reviewed earlier in the chapter are found with imprinting objects. For instance, in an analog of the experiment depicted in Figure 5.6, chicks imprinted to a visual pattern and later trained on a heat-reinforced discrimination between two patterns learned faster if the imprinting stimulus was one of the to-be-discriminated patterns (Honey, Horn, and Bateson 1993).

The conditioning analysis of imprinting is supported by evidence that imprinting objects are reinforcing. For example, chicks and ducklings will perform an instrumental response to get a view of an imprinting object (Bateson and Reese 1969; Hoffman and Ratner 1973) even before imprinting can have taken place. Since Pavlovian USs such as food also reinforce instrumental behavior, it seems reasonable to conclude that some feature of the imprinting object, such as motion, functions as a US in imprinting. Consistent with this view is evidence that an object whicht does not initially evoke any filial behavior comes to do so when the bird has seen it moving but not stationary (Hoffman 1978). In addition, features of the imprinting object should block or overshadow each other, as indeed they do in experiments using objects with separable parts (review in van Kampen 1996). However, the conditioning model also predicts that imprinting to a moving object will extinguish if the object is kept stationary. This does not happen, and on the perceptual learning view it should not. Also contrary to the conditioning model is the fact that filial behavior eventually develops to a sufficiently conspicuous stationary object (Eiserer 1980; Figure 5.10).

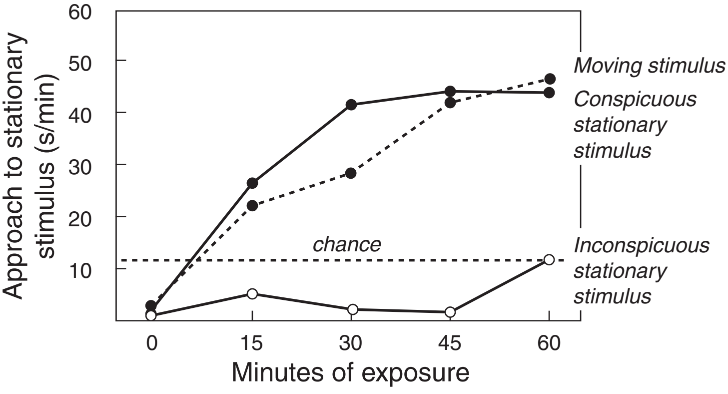


Figure 5.10. Mean time (in seconds per minute of test) ducklings spent approaching a stationary imprinting stimulus during three kinds of experience with it. Redrawn from Eiserer (1980) with permission.

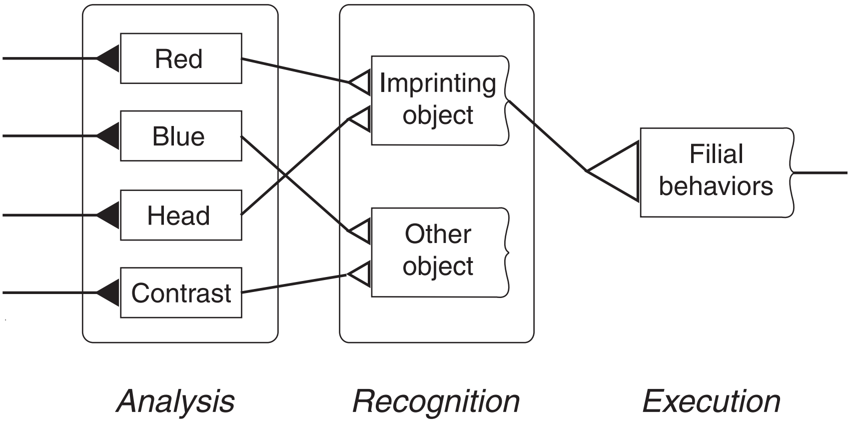


Figure 5.11. The "ARE" (Analysis, Recognition, Execution) model of imprinting. In this example the imprinting object is distinguished by being red and having a head. After P. Bateson (1990) with permission.

The contents of learning: A hybrid model

On the perceptual learning theory, what is learned in imprinting is a representation of the features of the imprinting object. On the conditioning model, it is an association of the neutral features of the imprinting object with its US-like features. Clearly, each theory uniquely explains some features of imprinting and omits others. For example, the perceptual learning model does not distinguish recognizing the imprinting object from recognizing anything else familiar. The conditioning model does not account for possible later effects of the imprinting experience like gradual learning of the imprinting object's features. Because perceptual learning about an object can be going on at the same time as associating the object with a US, both could be correct. This solution is proposed by the competitive exclusion model (P. Bateson 1990; Hollis, ten Cate and Bateson 1991; van Kampen 1996; P. Bateson 2000), according to which imprinting results in two kinds of learning: recognition of the individual imprinting object (perceptual learning) and connections of its representation to "the executive system" for filial behavior (S-R learning). It consists of three systems, corresponding to the perceptual, central, and motor aspects of any behavior system (Figure 2.7). Here these are analysis of incoming stimuli into features, recognition of familiar features, and execution of filial behavior patterns (Figure 5.11).

Conditions for learning: Summary

Filial imprinting is influenced by the same kinds of conditions that influence other learning about single events. Exactly how these factors matter differs among species (Goth and Hauber 2004). The discussion of whether imprinting is an example of classical conditioning (i.e., whether the conditions of learning include a positive contingency between neutral and US-like features) reduces to the question whether manipulations of the hypothesized CS-US relationship influence imprinting as predicted by conditioning theory. Clearly there is no single US such as motion, since young birds deprived of exposure to a conspicuous moving object will imprint to almost anything else eventually. One solution is to conclude that the "real" US is some feature shared by all effective imprinting objects such as arousing a particular affective state (Bolhuis, de Vos, and Kruijt 1990). This doesn't say much except that objects that support imprinting support imprinting. It also doesn't seem to explain non-conditioning-like aspects of imprinting such as failure to extinguish.

5.3.2 Effects of learning on behavior: Sexual imprinting

Like Pavlovian conditioning and some examples of habituation, imprinting endows a stimulus with control over a whole behavior system (van Kampen 1996). The behavior system is filial or attachment behavior, behavior that functions to keep the young bird close to its mother and the mother close to it. But one of Lorenz's claims for the uniqueness of imprinting was that it also influences behaviors which have not yet appeared at the time of learning, namely sexual behaviors. Contrary to Lorenz's claim, however, one might expect sexual preferences for conspecifics to develop without any specific experiences because mating with members of one's own species is essential to fitness.

Examples of sexual imprinting show that experience can in fact influence mate choice. The classic observation is Lorenz's (1935/1970; Immelmann 1972) report that hand-reared birds prefer to court humans even after years of social experience with their own species, including successful courtship and mating. But filial imprinting need not be directly responsible for sexual preferences. In filial imprinting the young bird needs to learn the characteristics of a particular individual, normally its mother, whereas species characteristics are what matter for mating. However, early learning about the mother could produce a generalized preference for individuals of the same species later on. If the mother is not present when the young are ready to mate, as in species where the young disperse from the natal area, the bird may choose the closest match it can find. In addition, fine details of the mother's appearance may be forgotten between infancy and maturity while salient features, characteristic of species members generally, are not (Zolman 1982). Moreover, the preference for the mother developed early in life need not be specifically sexual. The adolescent male may simply approach females of his species because they resemble his mother and thereby learn that they can provide sexual interactions (Bischof 1994).

The optimal outbreeding hypothesis

Attempts to distinguish sexual and filial imprinting experimentally have shown that filial and sexual imprinting can be dissociated in time. Vidal (1980) exposed domestic cockerels of three different ages to an object that could support both filial and sexual behavior. At sexual maturity, the birds that had been exposed to the model at the youngest age and shown most filial behavior showed the least sexual behavior to it. Those exposed latest and showing least filial behavior toward the model, showed most sexual behavior toward it. Sexual imprinting also occurs after filial imprinting in quail and ducks while birds are still in the family group but beginning to develop adult plumage (Bateson 1979). This timing may function to allow animals to learn the characteristics of siblings so they can choose mates slightly different from them. This combination of learning and choice mechanisms would promote an optimal degree of outbreeding, allowing animals to avoid the deleterious effects of breeding with very close relations without outbreeding so much as to dilute adaptations to local conditions. The representation of "close relative" should be based on siblings rather than mother alone because the siblings provide a larger sample of close relatives, one which includes characteristics of the father's family.

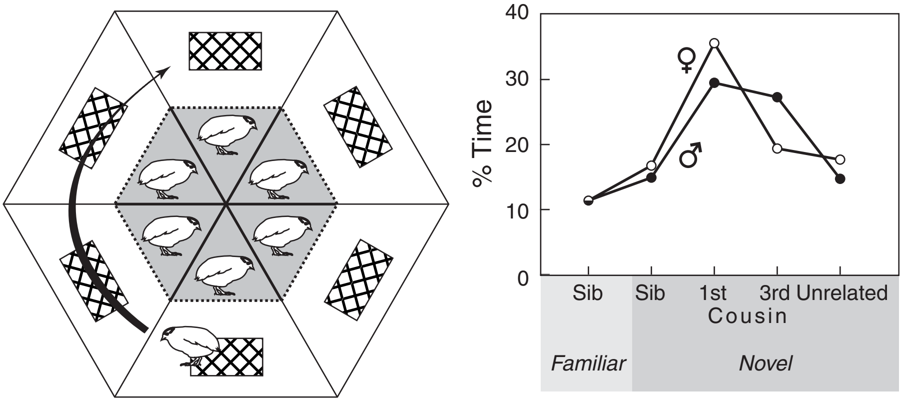


Figure 5.12. Overhead view of apparatus for testing sexual preference in quail and results when the stimulus animals were related to the subject as indicated. A pedal in front of each window (hatched rectangles) records how long the subject walking in the outer runway spends there. Redrawn from P. Bateson (1982) with permission.

Evidence consistent with the optimal outbreeding hypothesis comes from studies in which quail raised in family groups were exposed to siblings, cousins, and nonkin in the multiple choice apparatus shown in Figure 5.12. Birds of both sexes spent most time near first cousins (Bateson 1982). When quail of different degrees of relatedness were housed together after being raised in families, those housed with cousins layed fertile eggs sooner than those housed with siblings or more distant relatives (Bateson 1988), showing that preferences evident in the choice apparatus could have a real impact on reproduction. Mice and great tits also prefer mates slightly different from animals they were raised with (Barnard and Aldhous 1991; Boyse et al. 1991), but it is not clear how widely the optimal outbreeding hypothesis applies (Cooke and Davies 1983; Burley, Minor and Strachan 1990).

The content of learning

The optimal discrepancy model raises the question how information about different family members is represented: does the bird form a representation of a prototypical family member or does it store information about each individual (or exemplar) separately? This is a general question about category learning (Chapter 6). Prototype theory predicts that after training with a number of specific instances of a category, the *prototype* or central tendency will be preferred to any other instance, even if it is novel. Ten Cate (1987) tested this notion for "double imprinting" in zebra finches. (Notice that zebra finches are *altricial,* that is, they hatch naked and helpless. They do not need very early filial imprinting to keep them with the mother but may form sexual preferences while still in the family group.) If male zebra finches are raised by their own parents for about the first thirty days and then housed with Bengalese finches, some of them become "ditherers" (ten Cate 1986). They direct sexual behavior about equally to both zebra finches and Bengalese finches, although they prefer either to a novel species (Figure 5.13). Have such birds formed two separate representations of acceptable sexual partners or a single composite representation? Ten Cate (1987) tried to find out by offering them a choice between a zebra finch–Bengalese finch hybrid and a zebra finch or a Bengalese finch. If we assume that

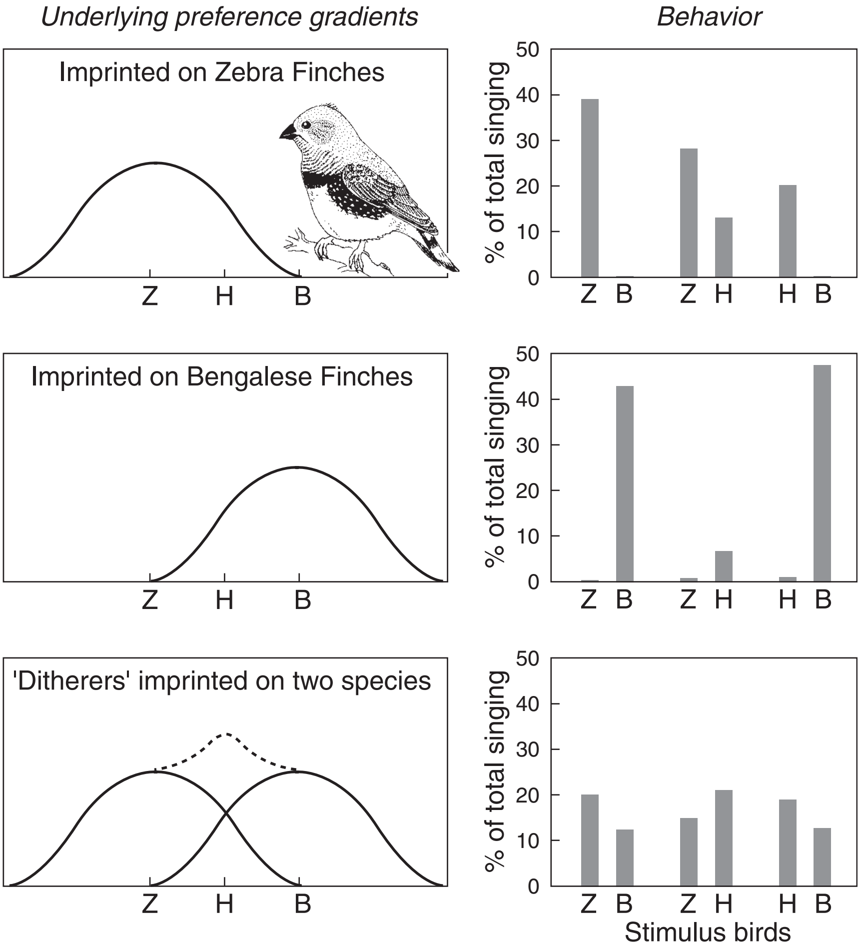


Figure 5.13. Panels on the left show hypothetical generalization of sexual preference in male zebra finches imprinted to zebra finches (Z), Bengalese finches (B), or on both species. In the latter case, the sum of the two preference gradients (dotted line) is maximal for a bird resembling a zebra finch–Bengalese finch hybrid (H). Panels on the right show sexual preference in pairwise tests with a zebra finch, a Bengalese finch, and a hybrid, measured as proportion of songs directed to each stimulus bird. Redrawn from ten Cate (1987) with permission.

the hybrid combines features of both species, prototype theory predicts that ditherers should prefer it to either a zebra finch or a Bengalese finch. But the same outcome is predicted by exemplar learning if generalization gradients from the two separate standards overlap enough (Figure 5.13). Ditherers did prefer the hybrid, and the results with birds imprinted on just one species indicated that such a preference could not result from summation of two separate generalization gradients (Figure 5.13). Thus the birds seemed to acquire a representation of a prototype. This research is a good example of how a framework for thinking about the development of representations may be transferred from one context (conditioning theory) to another (imprinting), although the conclusions from this study may not always apply (Vos, Prijs, and ten Cate 1993).

Sexual imprinting?

Some effect of experience on sexual preferences has been found in every species in which it has been looked for (ten Cate and Vos 1999), but in most cases the relative contributions of experiences and species-specific predispositions are unknown. Acquisition of sexual preferences would be a better term than sexual imprinting to summarize the effect of experience on what species an individual chooses to mate with because it is not a unitary learning phenomenon. In some cases (e.g., Gallagher 1977; Vidal 1980; ten Cate, Los, and Schilperood 1984) mere exposure to animals with certain characteristics influences later choice. In others, individuals have protracted and complex interactions with siblings and parents while sexual preferences may be being formed, making it next to impossible to isolate the experiences which are critical (if indeed any are) to later mate choice. For example, when young zebra finches are raised by foster parents consisting of a zebra finch and a Bengalese finch, the zebra finch parent directs more feeding and aggressive behavior toward the young zebra finches than does the Bengalese finch. The young may therefore pay more attention to the zebra finch parent and learn more about its appearance (ten Cate 1994). In addition, a preference developed during early life may be replaced by a preference for the first species the animal breeds with (Bischof 1994).

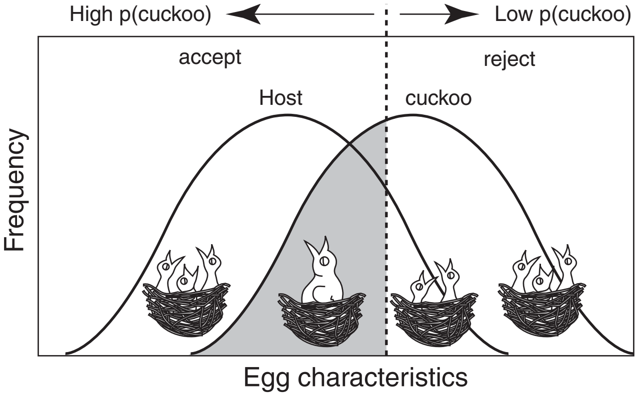
Species differences

Not all birds are raised by their own parents. For example, cowbirds and cuckoos are among species that are *brood parasites,* laying their eggs in other birds' nests and leaving them to be raised by their unfortunate foster parents (Box 5.2). Megapodes, large chicken-like birds of Australia and nearby islands, bury their eggs in the ground and the young hatch and dig their way out by themselves. How such birds recognize individuals of their own species for flocking and mating has been attracting attention more recently than the "classic" imprinting species (Goth and Hauber 2004). Indeed, functional notions about imprinting suggest many possibilities for comparative studies which have hardly been exploited.

Box 5.2 A Cost of Recognition

European cuckoos (*Cuculus canorus*) lay their eggs in other birds' nests. When the young cuckoo hatches, it pushes the eggs or young of its host out of the nest, thereby monopolizing all the host's parental effort while reducing the host's reproductive success to zero (Davies and Brooke 1988). It would seem that the small songbirds parasitized by cuckoos should be able to recognize their own eggs and/or offspring so they can discriminate against cuckoos. Some such birds do learn what their own eggs look like and reject eggs that are too different (Davies and Brooke 1988; Lotem, Nakamura, and Zahavi 1995). However, cuckoos' eggs are very good mimics of their hosts' eggs; different races (*gentes*) of cuckoos specialize on different host species and lay eggs that closely resemble the eggs of those hosts. Thus potential hosts faces a difficult signal detection problem, and their behavior can be understood in terms of the costs of and benefits of accepting versus rejecting unusual eggs in the nest (Figure B5.2; Davies, Brooke, and Kacelnik 1996). Ejecting an egg entails some risk of breaking or rejecting one's own egg. When the probability of parasitism is low, the host's expected reproductive success is highest with a relatively lax criterion for rejection, but when the probability of parasitism is high, the benefit of rejecting outweighs the cost, and potential hosts should discriminate more strongly against deviant eggs. Some birds adjust their criterion on a short-term basis: seeing a stuffed cuckoo on the edge of the nest increases reed warblers' tendency to reject a model cuckoo egg (Davies, Brooke, and Kacelnik 1996).

Figure B5.2. The decision to accept or reject eggs in the nest as a signal detection problem. Payoffs are represented as raising a full brood of one's own (three small nestlings), a reduced brood, or a cuckoo (single big nestling). The optimal placement of the decision criterion depends on the probability of cuckoos in the environment as indicated. After Davies, Brooke, and Kacelnik (1996) with permission.



Why doesn't this reasoning also apply to offspring recognition? One possibility is that any mechanism for rejecting parasites such as cuckoos requires that the hosts learn what their own offspring look like in the first place. A learning process like imprinting on the first brood of offspring raised would go wrong whenever the first clutch was parasitized: the parent would learn to accept cuckoos and reject all future offspring of its own (Lotem 1993). Here is a case where not learning is better than learning. Moreover, a small bird like a reed warbler can discriminate against cuckoos without recognizing them as something not their own young simply by abandoning its nest when the nestling has been there too long. The cartoon in Figure B5.2 with one large baby cuckoo nearly filling a nest built for several baby warblers is an accurate depiction of the relative sizes of cuckoo and host offspring. The big baby cuckoo takes longer to fledge than a brood of smaller birds, and it turns out that reed warbler hosts abandon young that have been in the nest unusually long. This is true whether there is only one offspring or as many as four (Grim 2007).

Bird species in which individuals nest close together and/or the young may wander should have mechanisms for parent-offspring recognition. Sometimes animals must make what seem to be incredibly difficult discriminations, as when penguins can find their offspring in a colony of hundreds or thousands (Aubin and Jouventin 2002). Such feats need not involve specializations in recognition learning ability. Cues to identity of the eggs or young could be very salient and/or the animals could have perceptual specializations for discriminating individual differences. Learning to recognize eggs and offspring has been studied comparatively in colonial and solitary-nesting gulls and swallows (Beecher 1990; Storey et al. 1992). In swallows, colonial and solitary species differ in the signals given off by the young rather than in adult perception or learning.

5.3.3 Imprinting: Conclusions

The essence of filial imprinting is that through mere exposure to a stimulus during a sensitive period the animal both learns its features and comes to preferentially direct filial behavior to it. The feature-learning part of imprinting seems to be the same as any perceptual learning, but its behavioral effects are specific to filial behavior. This makes filial imprinting distinct from a mere preference for the familiar, which is widespread among animals and reflects the fact that something previously experienced without aversive consequences is probably safer than something unknown. The fact that the imprinting experience endows the imprinting object with privileged access to the filial behavior system parallels the way in which conditioning endows CSs with control over feeding, sexual, fear, or other behavior systems (Chapter 4). What remains as unique to filial imprinting is its rapid occurrence through mere exposure early in life and—at least with naturalistic objects—the difficulty of reversing it. As well, its restriction to a comparatively few species gives it one property of a specialized learning module.

When it comes to sexual imprinting it is probably preferable to think in terms of a set of processes involved in acquisition of sexual preferences rather than a single imprinting-like process. We look a little further at some of these processes in the next section. The term *imprinting* has been extended to other preferences that appear to be formed early in life, most notably habitat preferences (see Davis and Stamps 2004). When young animals disperse from the place where they were born, choosing to settle in a place that is similar to the natal habitat makes sense because by virtue of its similarity such a place is likely to have the necessary resources for living and breeding. And indeed, there is experimental evidence from diverse species that animals prefer habitats like their natal habitats (Davis and Stamps 2004). However, "habitat preference" could actually be preference for any of a number of resources in the habitat, acquired in any of a number of ways, For example, the animal might settle where there an abundance of familiar food. Accordingly, the label *habitat imprinting* has been replaced by the more neutral term *natal habitat preference induction* (Davis and Stamps 2004).

5.4 The behavioral ecology of social recognition: Recognizing kin

Recognizing your mother and recognizing an appropriate mate are but two kinds of social recognition. Even some invertebrates such as wasps and hermit crabs show evidence of recognizing specific individuals, dominance hierarchies imply an ability to recognize individuals by rank (review in Tibbetts and Dale 2007), and many animals show social recognition in a variety of other contexts as well (Chapters 12 and 13). But the form of recognition most discussed by behavioral ecologists is *kin recognition,* that is, social recognition in which animals respond selectively to their relatives. Inbreeding avoidance, mentioned in the last section, requires discriminating against relatives, but in *nepotistic* situations animals help their relatives. For example, rather than leaving their parents' territory and starting their own families, Florida scrub jays and young of some other birds remain at home and help to feed their younger siblings (Woolfenden and Fitzpatrick 1984). Helping at the nest tends to occur when good territories are so scarce that young inexperienced birds are unlikely to be able to breed successfully on their own. The scrub jays' helping at the nest is an example of behavior that benefits close relatives and is therefore subject to *kin selection* (W. Hamilton 1963). Kin selection arises because what really counts in evolution is the *inclusive fitness* of an act, its effects on the actor's individual fitness plus its effects on the fitness of the actor's relatives in proportion to their relatedness (Box 1.2). For example, because siblings share half their genes with each other, behavior that increases two siblings' reproductive success more than it reduces the reproductive success of the altruist increases the altruist's inclusive fitness. This reasoning explains how scrub jays could be selected to stay at home and help when conditions are unfavorable for independent breeding.

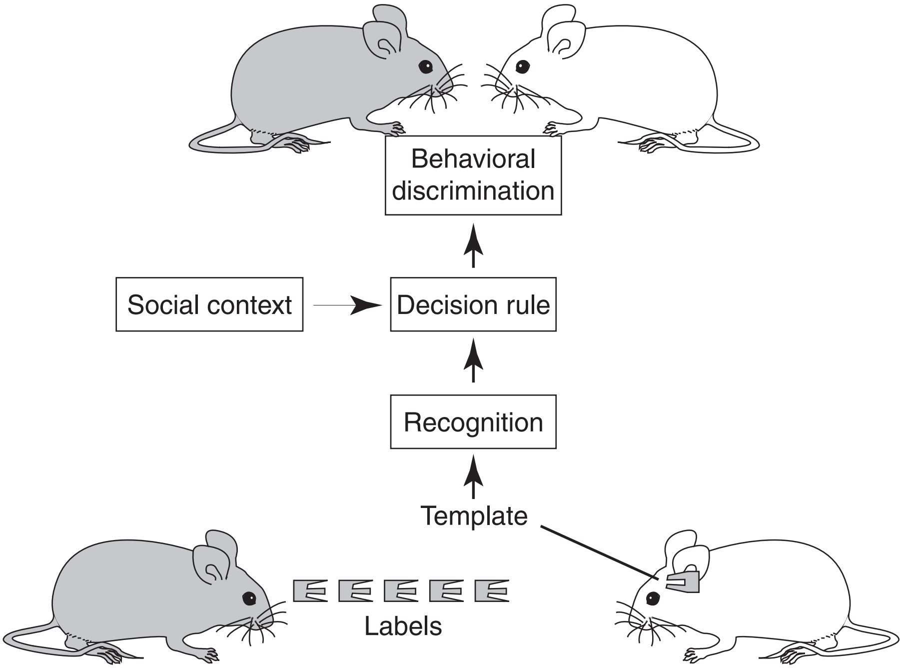


Figure 5.14. The elements of a recognition system. The white mouse recognizes the grey one as having the relevant label for a behavioral response. Adapted from Waldman, Frumhoff, and Sherman (1988) with permission.

Kin recognition has received a lot of attention from behavioral ecologists because it is expected whenever fitness is increased by directing resources selectively toward relatives. Figure 5.14 is a general depiction of social recognition systems that helps in thinking about the information processing it requires. A fundamental requirement is that the individuals to be discriminated must emit a distinctive signal (a “label”) that species members can perceive. Signals for discriminating kin should be reliable cues to the bearer’s genetic identity (Neff and Sherman 2002), but as we see in a minute this does not mean they have to be correlated with the animal’s genetic makeup as such. Perception of the signal must trigger an internal representation that corresponds to “relative,” the “template” in the figure. This sort of representation for the central tendency of a category is referred to as a *prototype* in Chapter 6, but *template* is used here to retain the flavor of the model in Figure 5.14.

Having detected whatever cues identify their kin, the perceiver directs some behavior selectively to them. The behavior shown and the threshold for showing it may depend on the social context (Reeve 1989; Mateo 2004). The distinction between detecting kin and discriminating in their favor is nicely underlined by a comparison of golden-mantled and Belding’s ground squirrels (Mateo 2002). As discussed later in this section, the very social Belding’s ground squirrels discriminate in favor of kin in a variety of situations whereas golden-mantled ground squirrels show little evidence of recognizing kin other than mothers and offspring. Nevertheless, in habituation-dishabituation tests, golden-mantled ground squirrels discriminate among the odors of grandmother, aunt, half-aunt, and non-kin in a graded way just as Belding’s ground squirrels do (Figure 5.15; Mateo 2002). In terms

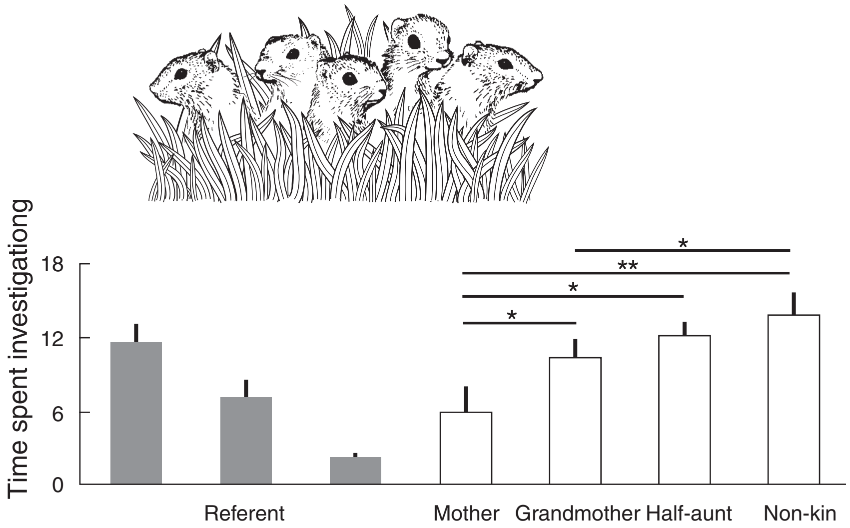


Figure 5.15. Time (mean seconds) Belding's ground squirrels spent investigating an object with the odor of an unfamiliar animal (referent) during successive presentations and the same measure from subsequent presentation of the odor of an individual related to the referent animal as indicated. Bars mark siginificant differences. Data from Mateo (2002), redrawn with permission; drawing after a photograph in Krebs and Davies (1993), with permission.

of Figure 5.14, they evidently possess kin labels and a recognition template, but the ability to discriminate along the dimension of relatedness does not modulate nepotistic behavior.

Kin recognition may be indirect: the altruist responds to a contextual stimulus normally correlated with kinship. For instance, parents of altricial young like many songbirds or small rodents are usually safe in responding to anything they find in their nest as if it is their offspring, for example by feeding it. Cuckoos, cowbirds, and other avian nest parasites exploit this rule by laying their eggs in other birds' nests. When the young cuckoo hatches, it pushes its foster siblings out of the nest, and the host birds unwittingly put all their reproductive effort into feeding the young cuckoo (Box 5.2). Following a simple rule like "treat everything in the nest as your offspring" does not require kin recognition nor learning the features of the offspring as such. Discrimination might be tied to location, so that a relative encountered elsewhere is treated as a stranger. For this reason, not all agree on whether indirect recognition should be regarded as a form of kin recognition (Tang-Martinez 2001; Mateo and Holmes 2004). Clearly, however, it functions to allow animals to discriminate in favor of kin and that sense is as good a kin recognition mechanism as any other.

When family members are together in the same nest or territory at a predictable time in the life cycle, the stage is set for learning that permits recognition outside that spatial context. In imprinting, for instance, newly hatched chicks and ducklings behave as if following the rule: "The first large moving object you see is your mother." This rule works because the mother is virtually certain to be near the nest when the babies hatch. The same kind of principle allows young animals to learn characteristics of their siblings while in the nest and later behave altruistically toward them. Such experience-based kin recognition has been studied extensively in ground squirrels and other rodents, where it is based on odor (R. Johnston 2003; Mateo 2003), and in some birds, where it is more often based on auditory or visual cues (e.g., Beecher 1990; Nakagawa and Waas 2004; Sharp. et al. 2005). In Belding's ground squirrels (*Spermophilus beldingi*), males disperse from the area where they were born, but adult females establish burrows close to their natal area (Holmes and Sherman 1982). Therefore, females often interact with their own offspring, their sisters, and the sisters' offspring, but males do not. As kin selection thinking predicts, closely related females behave altruistically toward each other in defense against predators and territorial disputes. For example, females are more likely to alarm call in the presence of sisters and offspring, a behavior that may increase their own risk of being caught by the predator.

The role of experience in kin recognition in this species has been investigated by means of *cross-fostering experiments* (see Mateo and Holmes 2004; Holmes and Mateo 2007). In such experiments, babies from one nest are raised in the nest of a foster mother along with babies to which they are unrelated. (Until the time when the young are ready to start leaving the nest, mothers accept foster babies and rear them as their own, that is, they use a location rule as a guide to kinship at this stage.) Kin recognition can then be tested by allowing two animals to meet in a neutral arena and recording the incidence of aggression and other behaviors. Such studies show that Belding's ground squirrels treat the animals they were raised with as kin. The learning involved could be sheer familiarization, as in habituation or perceptual learning. It could be imprinting-like, conferring a special social significance to stimuli experienced during a sensitive phase of development, or it could involve associating features of others in the nest with some US-like events (Tang-Martinez 2001; Mateo 2004).

When there are multiple siblings in the nest, the learning is essentially category learning, discussed in Chapter 6. Thus the resulting representation or recognition template might include features of each sibling or be like a prototype or average of "sibling" (Mateo and Holmes 2004). In general, it is difficult to distinguish these possibilities behaviorally, and notwithstanding some speculations about whether prototypes or exemplar memory are involved in kin recognition (Mateo 2004), there seems to be no relevant evidence one way or the other. Consistent with either kind of representation, ground squirrels generalize their learned representation of kin, treating new individuals like kin if they are similar to those in their natal nest. For example, unrelated females raised with each others' siblings are less aggressive toward each other as adults than are pairs of unfamiliar animals not raised with each others' relatives (Holmes 1986). Such generalization is based on the similarity of odors from genetically similar individuals (Holmes and Mateo 2007; Cheetham. et al. 2007). Indeed, tests in which ground squirrels were allowed to investigate odors from different individuals, much like the tests with hamsters described in Chapter 3, show that odors are perceived as more similar the more closely related the individuals they come from (Figure 5.15; R. Johnston 2003; Mateo 2003).

If odors carry cues to genetic relatedness (see Cheetham. et al. 2007), then unfamiliar individuals can be recognized as kin. For example, females respond altruistically to those genetically similar to themselves even if they have never encountered each other or their siblings before (Holmes 1986). Such behavior suggests that individuals respond to some signal directly linked to genes similar to their own. It could result from a single gene, or "recognition allele," controlling production of signal, recognition, and discriminative behavior, but this sort of single-gene control of multiple behavioral mechanisms is considered unlikely (Grafen 1990; Mateo 2004). A more likely, but controversial, possibility is that direct recognition of kin is based on comparing their characteristics to your own, a mechanism known as *self-referent* *phenotype matching* (Hauber and Sherman 2001). For example, because female Belding's ground squirrels may mate with more than one male, litters can contain both full siblings (same father and mother) and half siblings (same mother, different father). Who is who can be determined by DNA fingerprinting. Females raised with full and half sisters behave most altruistically toward their full sisters (Holmes and Sherman 1982), implying that genetic similarity is playing a role over and above familiarity.

A critical test of self-referent phenotype matching requires raising an animal apart from its relatives from birth and then seeing if it discriminates kin from non-kin (Hauber and Sherman 2001; see also Mateo and Holmes 2004). This has been done with positive results in golden hamsters (Mateo and Johnston 2000), peacocks (Petrie, Krupa, and Burke 1999), and cowbirds (Hauber, Sherman, and Paprika 2000). None of these experiments makes clear, however, whether the animal is matching cues from the stimulus animal to a learned representation of some aspect of itself or to on-line perception of its own characteristics. For example because cowbirds develop in the nest of another species, they could use self-referent phenotype matching to recognize which species to mate with when adult. When nestling cowbirds began to grow feathers, Hauber, Sherman, and Paprika (2000) colored some black and left others normal grayish-brown. When tested for preference between black-dyed and normal gray adults, colored birds preferred black females, whereas controls preferred undyed females. However, experimental birds were still black and the controls still gray at this time. Additional groups in which the subject birds were colored just before the test could help to unravel the roles of past experience versus perception of present appearance (see Tang-Martinez 2001).

5.5 Forms of recognition learning compared

Animals learn about events they are simply exposed to in the absence of specific contingencies with other events. The examples of recognition learning that have been analyzed most extensively are habituation, perceptual learning, and imprinting. In each case, the features of a stimulus likely become associated with each other so that exposure to one feature recalls other features, as described in Section 5.2 on perceptual learning. With the exception of the sensitive period in filial imprinting similar conditions are important for each kind of recognition learning. However the resulting behavioral changes are qualitatively different and are evident in more or less specific behavior systems. Perceptual learning is traditionally assessed by testing whether an arbitrary relationship is learned more readily with a familiar than with a novel stimulus. In habituation, a preexisting response decreases in probability or intensity. In imprinting, sexual or filial preferences develop. Comparator models have been prominent in accounts of recognition learning: present input is compared to a stored representation and responding is based on the discrepancy between them. Notwithstanding largely untested differences in the kinds of representations they imply, the models of the cognitive processes involved in recognition in habituation, imprinting, and kin discrimination are essentially the same, as can be seen by comparing Figures 5.5, 5.11, and 5.14.

The section of the chapter on social recognition describes some natural situations involving recognition of other individuals. In a few of them, something is known about what cues are used and how they acquire their significance. In most of these cases, too little is known about the conditions and contents of recognition learning to compare it in detail to the examples described earlier in the chapter. However, there seems to be no reason to question that the same sorts of learning are involved. For instance, in Belding's ground squirrels, phenotype matching of the individual's odor might be involved in initial recognition of kin, but distinctive features such as appearance and voice may later be associated with this feature to permit individuals to be recognized at a distance (see Box 5.1). The results of the many studies of how animals readily learn about the objects to which they are exposed in the laboratory make it plausible that similar learning contributes to the complex social knowledge underlying some animal societies (Chapter 12).

Further reading

Chapter 5 of Papini's (2008) text includes a comprehensive and well-illustrated introduction to habituation, including recent work on its neurobiology. Ethological observations of a wide range of examples are described by Hinde (1970a, Chapter 13). The book by Hall (1991), still the standard review of habituation and perceptual learning, develops an argument for an integrated model of habituation, latent inhibition, and perceptual learning. Hall (2001) updates it.

Lorenz's (1935/1970) own account of his work in imprinting is still very much worth reading. The most comprehensive review of imprinting remains that by Bolhuis (1991). There has been comparatively little recent behavioral work on filial imprinting (Bateson 2000), but it has continued to be studied at the neural level, as summarized by Horn (2004). A new direction in research on sexual imprinting is comparative work on species recognition by brood parasites, reviewed by Goth and Hauber (2004). The chapter by Sherman, Reeve, and Pfennig (1997) is a general discussion of recognition mechanisms. Mateo (2004) and R. Johnston (2003) provide substantial reviews of recent work, and Holmes and Mateo (2007) give a nice overview of research on kin recognition with particular reference to rodents. Tibbetts and Dale (2007) discuss individual recognition from a functional perspective, with many examples including wasps, lobsters, and cetaceans.

6

Discrimination, Classification, and Concepts

6.1 Three examples

1. A male stickleback with a bright red belly, ready to mate, swims about in a tank. A grayish model fish with a swollen "belly" appears, and our subject begins to display courtship movements. Their vigor increases when the model assumes a diagonal posture with its head up. A short time later, another model, with a red, unswollen, belly, is introduced. The male darts toward it, ready for a fight (Figure 6.1).

2. A female baboon hears another female in her troop make a threatening grunt and looks in the direction of the sound. The grunt is answered by the scream of a low ranking female from the caller's own family, and the listener resumes foraging. The next day, she hears the same female grunt, but this time the grunt is followed by the scream of a dominant female, and our listener looks toward the sounds for several seconds.

3. A pigeon pecks at a small photograph of Harvard Yard containing trees, buildings, people. After a few seconds, a hopper of grain appears and the pigeon eats. Now the scene changes to a treeless Manhattan street. The bird emits a few desultory pecks, then turns away and paces about. After a minute or so, a picture of a leafy suburban garden appears and the bird begins pecking again.

These animals are *discriminating* among model fish, sounds, or pictures. In operational terms, they are exhibiting *stimulus control.* At the same time they are *classifying* or *categorizing* complex stimuli, in that they give one response to some stimuli and different responses to others. This chapter asks what mechanisms underlie such behavior. When animals respond differently to different classes of things, does this mean they have an underlying concept? Does the stickleback, for example, have a concept of "mate" or "rival male"? Or can their behavior be explained as responses to a few simple stimuli? What do these apparently different explanations mean? And how does discriminative behavior develop?

Clearly, the issues here overlap with those in the chapters on perception, learning, and recognition. In general, in this chapter animals are discriminating among stimuli that they readily perceive as different. Chapter 5 was concerned with discriminative

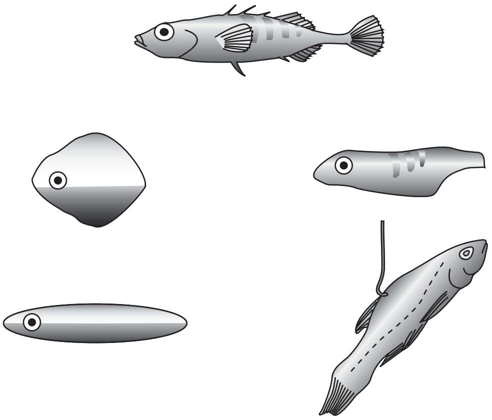


Figure 6.1. Model fish used to discover what stimuli control sexual and aggressive behaviors of male sticklebacks. Top: a normal male stickleback. Models on the left have red undersides, like normal males. On the right is a model with the swollen belly characteristic of egg-laden females and a dead tench presented in the upright posture of a courting female stickleback. Redrawn from Tinbergen (1951) with permission.

behavior acquired through simple exposure, whereas much of this chapter concerns explicit *discrimination training,* in which some stimuli are paired with one consequence and others, with another. Ideas about learning and event representation introduced in Chapters 4 and 5 are key to understanding the effect of such training, and they are elaborated here.

We start, however, with natural stimuli and discriminations that are not explicitly trained, as in Examples 1 and 2. Experience may contribute to what animals do in these situations, but the focus is on what aspects of natural objects control discriminative responding and how they do so, not on how it develops. Section 6.2 introduces classical ethological phenomena and ideas, and Section 6.3 reviews more recent analyses of how animals classify signals in the wild. Traditional discrimination training experiments used simple stimuli like tones and lights. Section 6.4 reviews the principles they reveal, and Box 6.3 discusses the role these principles play in the arms race between predators and prey. We then return to classification of complex stimuli in experiments on learned discriminations between categories of things like Example 3. Is animals' behavior in such experiments evidence that they have a concept or are they just clever memorizers? What does it mean to have a concept anyway?

As this preview suggests, animal discrimination and classification have been the subject of two rather separate research traditions. Laboratory research by psychologists has been—and continues to be—dominated by studies with pigeons like that depicted in Example 3. These are designed to test theories of visual category learning, many of them derived from studies with humans. Research like that depicted in Examples 1 and 2 is more concerned with discovering whether and how animals classify natural signals and other stimuli in biologically meaningful ways. Examples of what may be learned by integrating these approaches will be highlighted throughout the chapter.

6.2 Untrained responses to natural stimuli

6.2.1 Sign stimuli

One of the key observations of classical ethologists was that, like the stickleback in Example 1, animals respond selectively to objects in their environment. Among the wide range of stimuli that an animal's sense organs can detect, some elicit one behavior, some another. Patently perceptible features of natural objects are apparently ignored in some contexts. For example, male sticklebacks in breeding condition attack crude models with red bellies that lack most other fishlike characteristics. The red belly is a *sign stimulus*. Subtle features of sign stimuli can be important, however, particularly their configuration (see Ewert 2005). For instance, the red on the model is more effective if it is on the "belly," not the "back."

Sign stimuli may have their effects on very young animals or as soon as the animal can perform the appropriate responses, for example when it is ready to breed for the first time. Many of the stimulus-response connections appropriate for species-specific feeding, breeding, and other behaviors exist prefunctionally, but this need not mean that learning cannot occur later on nor that environmental conditions before they are first performed have no influence. That is, although the traditional concept of sign stimulus may have included innateness, the important fact that some stimuli selectively elicit highly specific responses survives the demise of the innate/learned distinction (see Chapter 1).

One way in which experience affects sign stimuli is to bring about control by subtle features of an object that are not effective originally. One well-analyzed example involves pecking at the parent's bill by gull chicks. Adult herring gulls have a red spot near the end of the lower mandible, and chicks' pecking at this spot stimulates the adult to regurgitate food. The red color of the spot is a sign stimulus (Hailman 1967). Newly hatched herring gulls seem to ignore features of model gull heads like shape and color and respond only to the presence of a red bill-like area (Figure 6.2). However, older chicks are also influenced by more subtle features like the shape of the head and peck more at more realistic models, reflecting a process Hailman (1967)

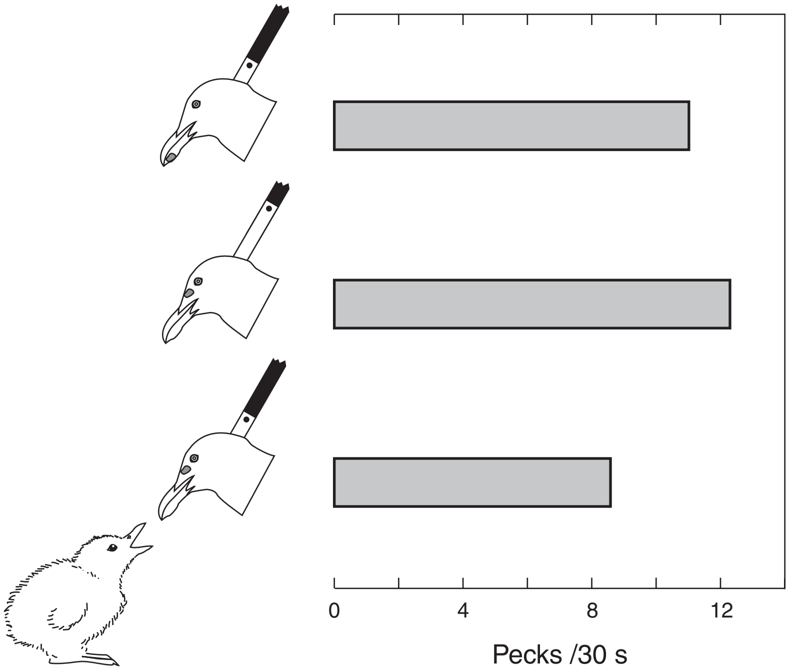


Figure 6.2. Effects of the placement of the red spot normally at the end of the parent's bill as in the top model and the point at which the model pivots (black dots) on pecking by herring gull chicks. Redrawn from Hailman (1967) with permission.

called *perceptual sharpening.* As in perceptual learning (Chapter 5), initially ineffective features of an object become associated with an effective feature so that objects originally treated as similar are differentiated. Indeed, young gulls learn to discriminate their own parents from other gulls by associating their visual and auditory features with the food reinforcement they provide (Griswold et al. 1995).

6.2.2 Multiple cues: Heterogeneous summation and supernormality

More than one feature of a natural stimulus may influence a given response. For example, a model's "posture" and its way of moving as well as its color determine how vigorously a male stickleback attacks it. Separable cues may have a precisely additive effect, a phenomenon known as *heterogeneous summation* (see Margolis et al. 1987; Ewert 2005). In an elegant example Heiligenberg (1974) measured aggression in the cichlid fish, *Haplochromis burtoni,* by observing how much one fish attacked smaller fish of another species living in its tank. The modest baseline level of attack could be temporarily raised or lowered by presenting a model conspecific outside the tank. A model with a black eye bar raised the level of attack; a similar model with orange spots but no eye bar reduced attack (Figure 6.3). These effects summed algebraically: a model with both a black eye bar and

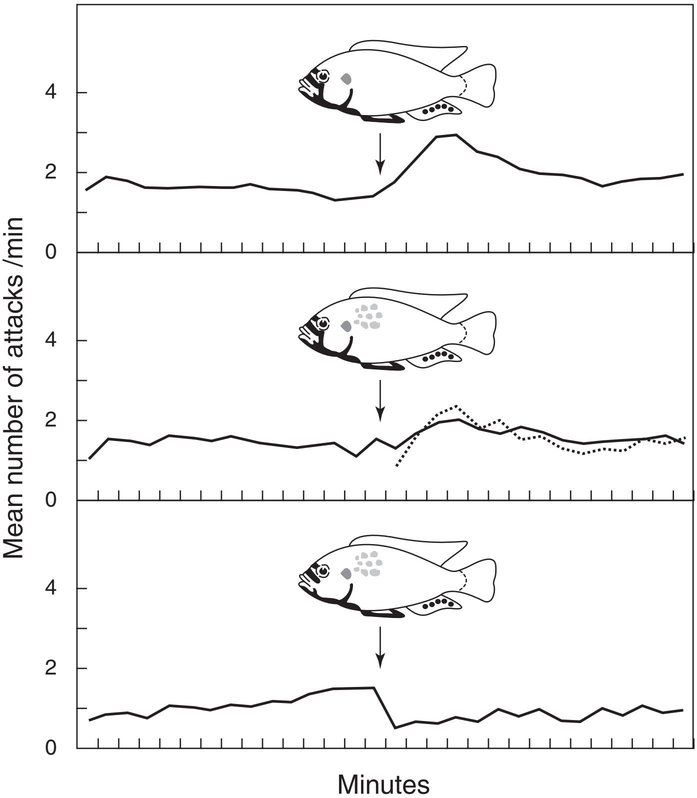


Figure 6.3. Summation of the inhibitory effect of orange spots (bottom panel) and the excitatory effect of a black eye bar (top panel) on attack rate of male cichlids, *Haplochromis burtoni.* Dotted line in the central panel is the sum of the curves in the two other panels; the solid line represents the data. Redrawn from Heiligenberg (1974) with permission.

orange spots caused little change in the attack rate. Sometimes stimuli with more extreme values than those found in nature are most effective. Baby herring gulls peck more at a red knitting needle than at the red spot on a parent's beak (Hailman 1967). As another example, incubating herring gulls retrieving eggs from outside the nest prefer eggs that are larger or more speckled than normal. Such extra-attractive characteristics can be combined in a single model to create a *supernormal stimulus* or *supernormal releaser* like that shown in Figure 3.10 (see also Section 6.4.2.; N. Tinbergen 1951; Baerends 1982).

Heterogeneous summation is analogous to the additivity of CSs in conditioning (Chapter 4). However, as in conditioning, separable cues are not always precisely additive (Partan 2004; Partan and Marler 2005). Features may form a configuration, psychologically different from the sum of its parts (Ewert 2005). Also as in conditioning (see Fetterman 1996), relative rather than absolute values of cues may be important. For instance, the optimal stimulus for begging in baby thrushes is a small "head" near the top of a larger "body." When a model has two "heads" near the top, more begging is directed toward the one that has the more nearly natural relative size (N. Tinbergen 1951). Some stimuli may not elicit responding in themselves but rather modulate responding to another stimulus, just as with occasion setting in conditioning.

The evolution, function, and use of multiple cues raises questions for behavioral ecologists (Fawcett and Johnstone 2003; Maynard Smith and Harper 2003), particularly in the context of mate choice (Candolin 2003; Phelps, Rand, and Ryan 2006). For instance, why do so many male birds invest in multiple signals such as brightly colored and long feathers plus singing plus displaying? All of these are not only energetically costly to produce but make males conspicuous to predators. Why do some male bowerbirds build elaborate avenues of sticks and decorate them with colored objects? Not only are such signals costly to males, females have been assumed to incur a cost in time and/or psychological resources when evaluating more than one feature of a signal. However, a consideration of "receiver psychology" (Rowe 1999) suggests that accuracy of detection, recognition, and discrimination should be enhanced rather than degraded by simultaneous presentation of multiple cues. Furthermore, multiple sexual signals can have several functions (Candolin 2003). They may signal different aspects of a male's quality or different features important in mate choice, particularly species membership versus individual identity (but see Phelps, Rand, and Ryan 2006). They might also be simultaneous redundant signals of the same thing, where "receiver psychology" may favor their evolution (Rowe 1999). In any case, sometimes different signals are used at different points in the mate choice process, as when a female is attracted by song from a distance and then responds to visual signals as she approaches the singing male. Such sequential use of cues is undoubtedly important functionally but it is less interesting mechanistically than simultaneous processing of multiple cues.

Multiple signals are also important in other forms of social recognition and in prey choice (Rowe 1999; Fawcett and Johnstone 2003; Partan 2004). Enhanced response to simultaneous cues in more than one modality, as to the song and sight of a displaying male, is an example of multisensory integration, a topic of active research in cognitive neuroscience (Calvert, Spence, and Stein 2004) and has attracted interest on that account (Partan 2004). So far, however, more attention has been given to documenting and classifying examples of such phenomena (e.g., Partan and Marler 2005) than to probing whether they have any special mechanistic properties (see Candolin 2003). Research like that on unimodal multicomponent signals described in Section 6.3 might be helpful in showing how different components are weighted in determining a response, perhaps by combining psychophysical theories about how different sources of information should be weighted (see Section 8.2.2) with evolutionary models of optimal cue use (Fawcett and Johnstone 2003; Phelps, Rand, and Ryan 2006).

6.2.3 Conclusions

Ethological terms like *sign stimulus* and *releaser* summarize important facts about animal behavior, but few researchers still use them. One reason is that the analysis of sign stimuli was intimately related to the Lorenzian model of motivation, now considered by many to be oversimplified and unrealistic (but see Hogan 2005). Sign stimuli were assumed to release accumulated *action-specific energy* via a species-specific decision mechanism, the *innate releasing mechanism* or *IRM*. One objectionable feature of this scheme was the term *innate*. As discussed in Chapter 1, this term fell out of use as all involved in debating it accepted that both environmental and genetic factors contribute to all behavior. Nevertheless, whatever it is called, untrained discriminative behavior shares many features with explicitly trained discriminations. These include the following.

1. Not all features of a relevant situation or object control behavior equally, even though all might be perceptible by the animals involved.
2. Features that do influence behavior have may have additive effects as CSs do. Conditional control and control by configurations or relationships may also be seen (Partan and Marler 2005).
3. Stimuli other than those that occur in nature may be more effective than natural objects. This describes supernormality as well as peak shift in trained discriminations (Section 6.4.2).
4. Discriminative behavior may be specific to relevant motivational states. For example, a male stickleback does not behave so differently toward males and females when he is not in reproductive condition. Similarly, stimuli associated with food may no longer evoke CRs in sated animals, evidence that the CS evokes a representation of the features of the US which then controls action (see Section 4.5.1).

6.3 Classifying complex natural stimuli

6.3.1 Classifying multidimensional signals in the field

Features of a sign stimulus are not always precisely additive, nor are they as simple as a red belly or a black stripe. For example, bird songs are complex temporal patterns of sound frequencies analyzable into notes and phrases. One approach to understanding behavior toward such complex stimuli represents them as points in a multidimensional stimulus space. For example, Nelson and Marler (1990) tested the hypothesis that birds identify the songs of their species by relying on the features that best distinguish them from the songs of other species found in the same habitat, the local *sound environment*. They studied two North American songbirds, the field sparrow (*Spizella pusilla*) and the chipping sparrow (*S. passerina*) by analyzing a number of parameters of the songs of these and 11 other species commonly singing around them in upstate New York. Many *exemplars* (i.e., specific examples) of each species' song were described along dimensions such as maximum and minimum sound frequency, number of notes, and note and song duration. When the average song of each species and its range of variation were placed in the multidimensional *signal space* so defined, three variables were sufficient to differentiate chipping sparrow song from those of the other species, while four additional variables were needed for field sparrow song, that is, this song overlapped with more of the other songs in the signal space (Figure 6.4).

To discover whether field sparrows actually use the features that best discriminate their species-typical song in signal space, Nelson and Marler observed the birds' aggressive responses to songs played in the middle of their territories. A standard species-typical song with median values of all features was compared to a song differing in just one feature. The feature being tested, note duration for example, was altered until the test signal reliably elicited less territorial threat than the normal song. The difference from normal defined the *just meaningful difference* (*JMD*) for that feature. In general, birds responded less to an altered song when its features took on values about 2.5 standard deviations away or more from the average value for the species. The just meaningful difference is most likely larger than the psychophysical just noticeable difference (JND, Chapter 3), that is, the birds could probably be trained to make much finer discriminations.

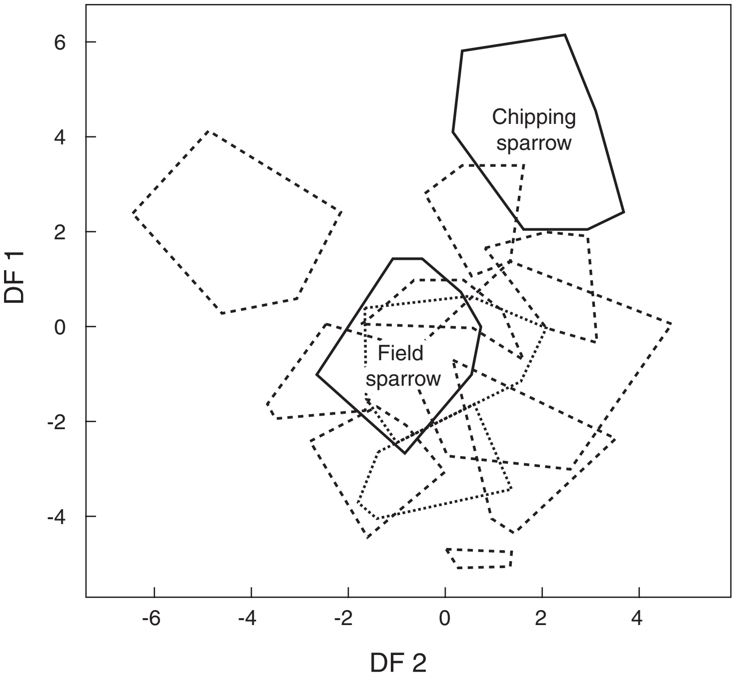


Figure 6.4. Two-dimensional space of song characteristics showing the extent to which chipping sparrow and song sparrow songs are similar to those of 11 other species found in the same habitat. Polygons enclose all songs sampled for each species. Dimension DF1 is positively correlated with song duration and number of notes; DF2 is correlated positively with minimum frequency and negatively with internote interval and note duration. Redrawn from Nelson and Marler (1990) with permission.

To find out how features were weighted in the birds' decisions, Nelson and Marler used two altered songs in each test. For example, a song with its maximum frequency altered by one JMD was pitted against one with its duration altered by one JMD. If the bird directed more aggressive behavior toward the song with altered duration than toward the song with altered frequency, it could be concluded that duration was less important than frequency in the classification of song as "field sparrow" versus "other species". Sound frequency was the most important feature for field sparrows, consistent with the hypothesis that birds should be most responsive to features that best differentiate their song from others in the same sound environment (see Figure 6.4). Other features were ranked in a way consistent with the hypothesis that species recognition is based on the least variable features of species-specific signals.

6.3.2 Birds classifying signals in the laboratory

A thorough multidimensional analysis requires large amounts of data from standardized tests, and these may be difficult to obtain in the field. Operant tests in the laboratory overcome this limitation. In one useful paradigm, the animal performs one response to present a steady background stimulus against which a second stimulus sometimes appears. The animal is reinforced for performing a second response when the different stimulus appears, and its latency to report "different" is taken as evidence of the ease with which it perceives the difference. A relatively large set of stimuli is used, maybe a dozen or more, and each appears sometimes as background and sometimes as the alternated stimulus. The data are converted into a representation of psychological distances among the stimuli in a multidimensional space: pairs of stimuli for which "different" is reported quickly are far apart, while pairs for which the latency is long are close together, that is, perceived as similar. Each cluster of stimuli in such a space defines a psychological category (for further discussion see Blough 2001). Unlike the method of category discrimination training discussed in Section 6.5, this procedure allows the animal to show how it classifies the stimuli on its own rather than imposing a classification scheme on it. The two approaches can be combined, as in the studies with bird song discussed in Section 6.5.5.

Dooling and his collaborators exploited this technique to study how birds classify vocalizations of their own and other species (Dooling et al. 1990; Dooling et al. 1996). For example, Dooling, Brown, Klump, and Okanoya (1992) tested canaries, zebra finches, budgerigars and starlings with the contact calls of canaries, zebra finches, and budgerigars. For each species of subjects, the sounds formed three clusters in multidimensional stimulus space corresponding to the three species' calls (Figure 6.5). When it came to detecting differences within species, the canaries, zebra finches, and budgerigars were each quickest at detecting differences between individuals of their own species. Psychophysical studies indicate that this species-specific advantage does not reflect differences in auditory perception but rather more central processing, in which calls are compared to a representation of a species-typical call and close matches are treated as belonging to the subjects' own species (Dooling 2004).

A similar study with primates (Brown, Sinnott, and Kressley 1994) showed that humans and Sykes's monkeys (*Circopithecus albogularis*) classified monkey and bird alarm calls as predicted on functional grounds. In the wild, the monkeys should respond similarly to all monkey species' alarm chirps because any of them could signal a predator, but they should ignore the acoustically similar chirping of forest birds.

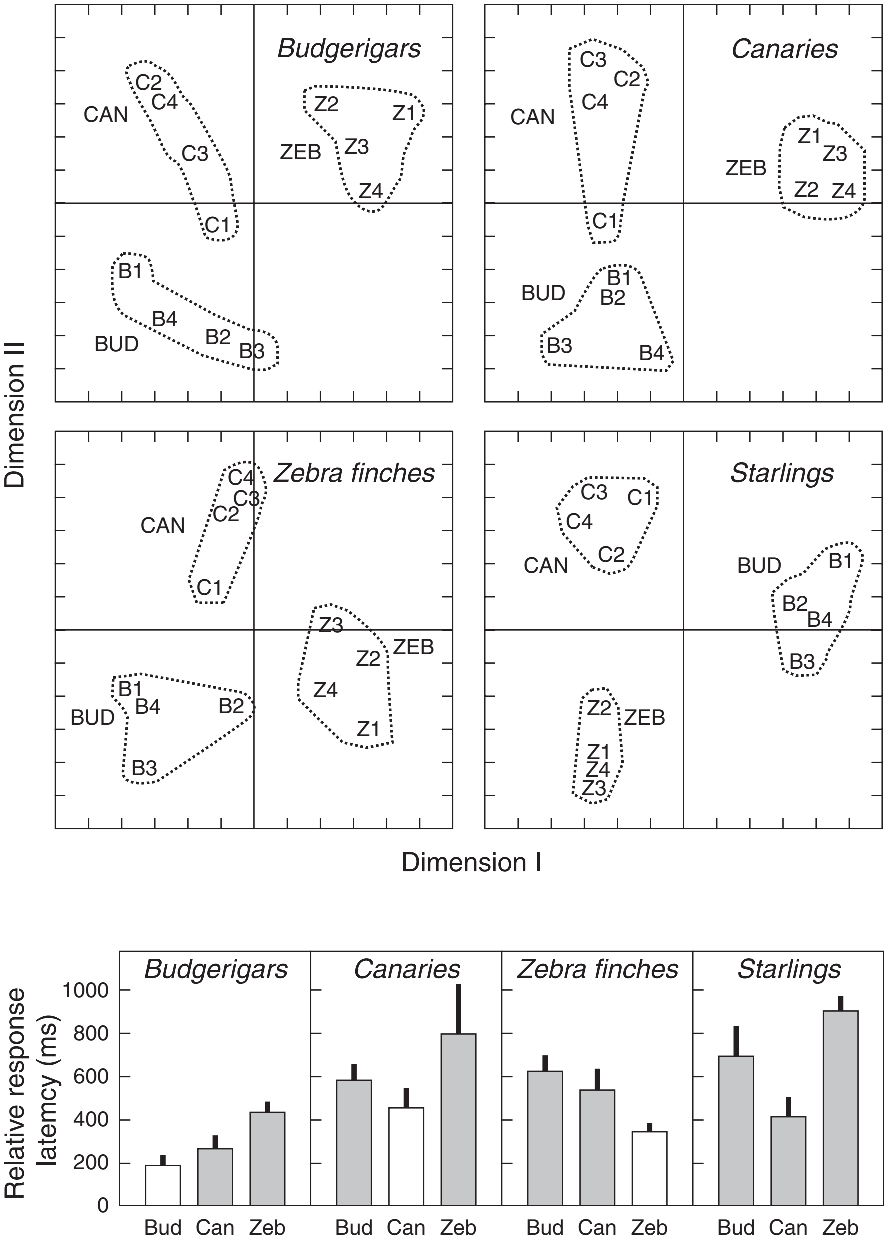


Figure 6.5. Top: Plots similar to that in Figure 6.4 showing how budgerigars, canaries, zebra finches, and starlings classified the songs of four canaries (C1–C4), four budgerigars (B1–B4) and four zebra finches (Z1–Z4). Lower panels: Latency with which birds of the four species tested responded when the test stimulus changed from one song to the song of another individual of the same species. Response to vocalizations of the subject's own species shown in white. Redrawn from Dooling et al. (1992) with permission.

Accordingly, Sykes's monkeys classified alarm chirps of their own and another sympatric monkey species as more similar to each other than either was to a sample of bird calls. People tested in the same way classified the bird calls as more similar to those of

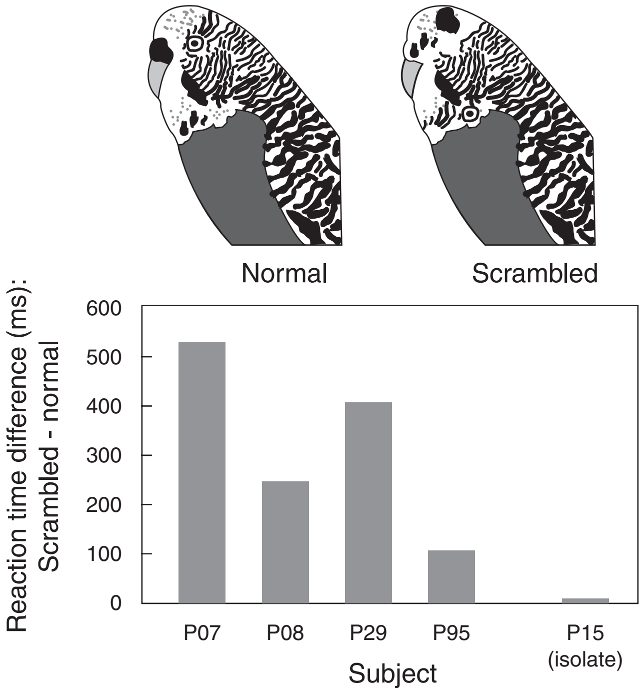


Figure 6.6. Normal and scrambled budgerigar faces used to test face perception in budgerigars. Data are the increase in latency when individual budgerigars were required to discriminate between scrambled faces compared to their latency to discriminate between two normal faces. The isolate was raised apart from other budgerigars. Redrawn from Brown and Dooling (1993) with permission.

monkeys and the monkey calls as more different from one another than the monkeys did. As another example of a species-specific advantage in auditory classification, birds of a number of species outperform humans when tones in one range of frequencies are to be discriminated from higher and lower tones. The birds discriminate the category boundary much more sharply than the humans do, showing evidence of the absolute pitch presumably used in song learning and recognition in the wild (Weisman et al. 2006).

Such comparative data on classification raise many questions. For example, would monkeys raised in the laboratory classify bird and monkey calls in the same way as monkeys that had lived in the wild? Conversely, would a naturalist with a lot of experience in the monkeys' habitat classify the calls as monkeys do? In Chapter 14 we see that many animals learn functional categories consisting of the alarm calls of other species in their habitat and thereby warn each other of a common danger. To what extent is the monkeys' response in these experiments due to this kind of experience as opposed to a perceptual specialization? We also need to be sure that animals treat sounds in an artificial context like an operant chamber as species-specific signals. There is some evidence that birds working for food in the laboratory do treat recorded species-specific vocalizations as vocalizations in that zebra finches learn an operant discrimination between zebra finch songs faster than birds not in reproductive condition (Cynx and Nottebohm 1992). Similarly, captive cottontop tamarins (*Saguinus oedipus,* a small monkey) reply to recorded tamarin long calls just as they do to the actual calls (Miller, Iguina, and Hauser 2005).

From a nonhuman perceiver's point of view, visual images in photographs and video may not match the real things very well (Box 6.1). Nevertheless, Brown and Dooling (1992, 1993) have successfully used colored slides in a procedure like the one used with auditory stimuli to analyze how budgerigars classify the faces of budgerigars and other birds. The birds classified slides of natural budgerigar faces on the basis of features that would be socially significant in the wild. They did not seem to be influenced by purely pictorial features like the proportion of the slide occupied by the image, suggesting that they were processing the slides as bird faces. Moreover, as with vocalizations, there was a species-specific advantage: budgerigars detected a difference between budgerigar faces quicker than one between zebra finch faces, although people judged zebra finches to differ more. In addition, studies with scrambled budgerigar faces indicated that the configuration of features into a face was important.

Box 6.1 How Do Animals See Pictures?

Following Herrnstein's (1979) demonstration that pigeons could acquire and generalize a discrimination between pictures with trees and pictures without trees (Example 3 at the beginning of the chapter), Herrnstein and de Villiers (1980) asked how pigeons perform when slides of fish—a natural category irrelevant to present-day pigeons—are used instead. This experiment is interesting only on the assumption that pigeons recognize objects and scenes in back-projected colored slides as such. If all the pigeon sees is an array of colored blobs, discrimination learning should not be affected by whether the slides depict objects natural or unnatural to pigeons' environment, or indeed whether they depict objects at all, and it was not. In retrospect, the notion that slides of objects and scenes are more naturalistic or ecologically valid stimuli than simple patterns and colors because animals see them as depicting places and things in the real world appears naive and misguided (Fetterman 1996; Delius et al. 2000; Fagot 2000).

How animals behave toward still or moving pictures has been addressed in two remarkably separate bodies of work. Some psychologists have continued on from Herrnstein using operant techniques to study aspects of picture perception in animals, mostly pigeons but also monkeys (Fagot 2000). One approach is to see if a learned discrimination transfers between arbitrary objects or scenes to images of them, or the reverse, to test whether objects and pictures are in some sense equivalent. The results have been mixed (Delius et al. 2000; Fagot, Martin-Malivel, and Depy 2000; Watanabe 2000). For example, pigeons trained to find food in a distinctive part of a large room seemed to transfer this discrimination to slides of different parts of the room (Cole and Honig 1994), but exposure to a particular outdoor location did not speed learning of a discrimination between slides of it and a second outdoor location (Dawkins et al. 1996; but see Wilkie 2000). A number of factors mitigate against transfer (D'eath 1998), including that slides or video may not capture color as seen by pigeons (see Box 3.1), and that they may be at unnatural viewing distances for the real objects they depict (Dawkins and Woodington 1997). Tests of transfer between objects and pictures of them also fail to take into account that real objects provide many cues to depth and distance unavailable in pictures (see Dawkins et al. 1996, for further discussion). Other research (Spetch and Friedman 2006) has looked at whether purely pictorial features important for object recognition in humans are also used by pigeons to classify drawings of objects. The results may or may not reveal something about general mechanisms of object recognition.

In a novel and potentially useful approach to testing whether animals relate pictures to representations of the real thing Aust and Huber (2006) trained pigeons to discriminate slides with versus without people using slides which never showed a particular part of the body, either hands or heads. If the birds saw the slides as representing parts of people, they should generalize to slides showing the missing part, for example, to a head alone for the group trained on headless people, but they should not generalize if they saw the slides as meaningless patterns. The birds did generalize to some extent, pecking more at slides with the missing part than to novel slides without any part of a person, and various controls suggested that no simple visual features of the slides could account for this. A nice further control would be a similar experiment manipulating parts of something pigeons are unfamiliar with.

Meanwhile, behavioral ecologists and ethologists have had a lively debate about the use of video playbacks in one twenty-first-century version of sign stimulus research with diverse species including spiders, lizards, fish, and birds. Videos of sexual, aggressive, and other behaviors have tremendous potential for revealing the cues animals use in social interactions because the behaviors and features of the animal in the video can be controlled and manipulated, even in an interactive way. However, not only do moving pictures have all the limitations of still pictures already mentioned, in addition some animals' flicker fusion frequency is higher than humans,' which means that what we see as smooth motion is likely perceived as jerky and perhaps aversive (see Adret 1997; D'eath 1998). Recent technical advances in producing and displaying computerized images have overcome many of these problems. Studies making use of them have shown, for example, that Japanese quail recognize a video image of a particular individual quail they saw "in person" earlier (Ophir and Galef 2003) and that Jacky dragons, a species of small lizard, display aggressively to a video rival exactly as to a real one (Ord et al. 2002). Increasingly robots are used to reveal the stimuli important in social interactions as they can even be deployed in the field. One way to be sure their visual properties are realistic from the perceiver's point of view is to cover them with real skin or feathers as done by Patricelli, Coleman, and Borgia (2006).

In summary, the best answer to the question asked by this box is, "It depends"—on the species of animal and the kind of discrimination being tested. Jumping spiders court conspecifics and attack prey that they see on TV, apparently not discriminating a video image from the real thing (Clark and Uetz 1990). Even with older types of video, chickens behave as if seeing real conspecifics and predators, apparently reacting to simple sign stimuli such as shape or motion. When used with appropriate caution, slides and video images of real-world things and events can be extremely useful for answering certain questions about how animals discriminate and classify things of importance in nature. The work on face recognition in budgerigars and other species described earlier in this chapter is one example; another is that on vocal communication in chickens discussed in Chapter 14.

Independently of this kind of research, numerous studies of category learning in pigeons like Example 3 (see Section 6.5) have used images of human faces as stimuli. Some of this work has looked at the importance of parts and their configurations in the birds' ability to respond differently to different sets of photographs such as male versus female faces. Face images have generally been used here simply as arbitrary patterns that can be varied in a systematic way with readily available morphing algorithms. Arguably, the results of such studies have only tenuous relevance to either pigeons' or humans' natural classifications, especially given some of the findings described next.

Monkeys, chimpanzees, and sheep can discriminate between individual conspecifics' faces in photographs (Kendrick et al. 1995; Parr et al. 2000). In humans, facial features in a normal configuration are thought to tap into a specialized face-recognition system. Some evidence for this is the observation that individuals' faces become more difficult to recognize when they are upside down. However, baboons trained to respond differently to images of two different familiar caretakers' faces showed no evidence for differential processing of upright versus inverted faces. Rather, they appeared to treat them as meaningless shapes (Martin-Malivel and Fagot 2001). Consistent with this conclusion are the results of a clever comparative study in which both humans and baboons classified black and white images as the faces of humans or baboons (Martin-Malivel et al. 2006). Once subjects succeeded with a set of 60 training images, they were exposed to computer-generated human-baboon morphs and degraded faces. Analysis of how such images were classified as a function of how they were degraded revealed that the baboons used the information in the images as would an observer treating the images as abstract shapes, whereas the humans referred them to preexisting concepts of baboon and human faces. Unlike tests varying features, such as eyes, that should be important for recognition, this method does not rest on any assumptions about what features are used. However, notwithstanding the conclusion suggested by this experiment, under some circumstances individuals of various primate species, including chimpanzees and rhesus macaques, do treat images of conspecific faces as such. For example, chimpanzees and rhesus match the facial expressions naturally associated with distinctive vocalizations to those vocalizations (Parr et al. 2000; Ghazanfar and Logothetis 2003; Parr 2003).

6.4 Discrimination learning

Discrimination learning traditionally refers to the results of procedures in which animals are reinforced for performing a different, arbitrary, response to each of two or more stimuli. Training with a single stimulus requires discrimination learning too, since the animal has to discriminate the experimental context plus the reinforced stimulus from the context alone. Methods of training with two or more stimuli (Box 6.2) have led to a distinctive body of data and theory with implications for the nature of animal category or concept learning. The discrimination training procedures described in Box 6.2 may suggest that they all involve instrumental training, that is, associating responses rather than stimuli with their consequences. However, procedures the experimenter views as instrumental may be effective because of the Pavlovian contingencies embedded in them. For example, as we have seen in Chapter 4, approaching a stimulus paired with food and retreating from one not paired with expected food are natural outcomes of Pavlovian conditioning procedures. Contemporary discussions typically apply to discrimination training in general. In any case, although theories about the content of instrumental learning are not discussed until Chapter 11, for present purposes it is necessary to know only how instrumental procedures are used to discover how animals discriminate and classify stimuli.

Box 6.2 Methods for Discrimination Training

Stimuli to be discriminated may be *simultaneous* or *successive*. For example, in a simultaneous black-white discrimination in a T-maze a rat chooses between a black arm and a white one, with black sometimes on the left, sometimes on the right. The rat might receive food in the white arm, no food in the black arm. Gradually it learns to enter the white arm regardless of which side it is on. In a comparable successive black-white discrimination the rat is placed in a black alley on some trials and a white alley on others. It finds food only at the end of the white (or the black) alley. In this *go/no go* discrimination, performance is assessed by comparing running speeds or latencies to reach the end of the white vs. black alleys.

Correction procedures can be helpful in exposing animals to to-be-learned contingencies: if the animal makes an unrewarded choice at the beginning of the trial, it is “corrected” by removing opportunity for all but the rewarded response. In simultaneous discriminations, there is always a correct, rewarded, response, and this may make these procedures more sensitive for detecting the early stages of learning with difficult discriminations because the animal never has to withhold responding.

Much of the older literature on discrimination training (see Mackintosh 1974) used rats in alleys and mazes, as described above. Now computer-controlled operant chambers are widely used because they allow automated testing of large numbers of animals for large numbers of trials. Pigeons are popular subjects because their visual acuity and color vision means they can be trained on tasks involving large numbers of visual stimuli. Operant procedures may have *discrete trials* as in the T-maze and runway, but *free operant* procedures are also used. In these, one or another of the stimuli to be discriminated is always available and response rates are compared in the different stimulus-reward conditions. A successive free-operant discrimination procedure is also referred to as a *multiple schedule*. Simultaneous free-operant discriminations are *concurrent schedules*. *Intermittent reinforcement* may be scheduled with a different frequency or pattern in the presence of each stimulus and response rates compared. It is not necessary that one of the stimuli be completely unrewarded; with sufficient exposure animals can learn quite subtle differences between reinforcement contingencies paired with different stimuli. They sometimes learn all sorts of other things the experimenter may not intend, too. For instance, in a successive free-operant discrimination with intermittent reinforcement in the presence of one stimulus and no reinforcement (extinction) in the presence of the other, animals can use the presence or absence of reinforcement in the first few seconds of each stimulus presentation as a cue to whether to keep responding during that stimulus.

Once animals have acquired a discrimination they may be tested to see which aspects of the discriminative stimuli control responding, as in the studies of generalization in Section 6.4.2. But animals don’t stop learning just because the experimenter is giving a test. Reinforcing the animal for any response it makes in the test may teach it to respond indiscriminately, but never reinforcing it for responding to the novel test stimuli is no better. A common solution to this dilemma is to reinforce responding intermittently during the training phase, as in the study by Blough described in Section 6.4.2. Intermittent or *partial reinforcement* for correct responses increases *resistance to extinction* (i.e., the animal will keep responding longer without reinforcement) and makes it possible to sneak in occasional unreinforced test stimuli without the animal learning not to respond to them, thereby increasing the number of tests that can be given.

6.4.1 Acquisition

Simple discriminations

Even in a novel environment a frightened rat runs into a black compartment rather than into a white one. It clearly discriminates black from white already, yet if experimentally naive rats are trained in a black-white discrimination with food reward, many trials may elapse before they perform differently from chance. This is not surprising if we consider that the situation is initially completely novel. Before the animal can become interested in eating and learn how to get food, its tendency to explore the novel environment and/or its fear of it has to habituate. This learning may occupy a separate phase of pretraining, or feeder training (sometimes called *magazine training*). In two-choice situations, animals commonly adopt *position habits* during the acquisition phase, or *presolution period*. For instance, a rat being trained on a simultaneous black-white discrimination may always choose the stimulus on the left. Historically, this kind of consistent response to incorrect features was called *hypothesis testing*, as if the animal was testing the hypothesis “left is correct.” Considerable debate was devoted to the question whether animals learn anything about the correct features during this phase (see Mackintosh 1974).

Not surprisingly, physical similarity between the stimuli to be discriminated influences the speed of discrimination learning. A discrimination between two shades of grey is learned more slowly than one between black and white. If the stimuli to be discriminated differ in several features, providing redundant cues, acquisition is faster than if they differ in only one feature (Mackintosh 1974). Animals may learn a difficult discrimination faster if they first learn an easy related one, as in the study of bats' auditory sensitivity described in Chapter 3.

Relative validity

Consider the following experiment on eyelid conditioning in rabbits (Wagner et al. 1968; Figure 6.7). (In eyelid conditioning, a CS signals a puff of air or a mild shock to the eyelid; the rabbit closes the nictitating membrane over its eye in anticipation of the US.) Two groups of rabbits were each exposed to two tone CSs, T1 and T2. Both tones were always presented in compound with a light, L. In the *uncorrelated group,* T1 + L and T2 + L were each followed by the US on 50% of trials. In the *correlated group* , T1 + L was always reinforced and T2 + L was never reinforced. Notice that the light was followed by the US half the time for both groups. If the number of pairings of light with the US is all that matters in learning to discriminate the light from the context alone, all the rabbits should respond similarly on test trials with the light alone. In fact, however, only the animals in the uncorrelated group showed substantial numbers of CRs to the light alone. This group blinked rather little to either of the tones alone (Figure 6.7). In contrast, rabbits in the correlated group responded to T1 and not to T2 or L alone. This pattern of results and others like it in instrumental paradigms (Mackintosh 1983) is accounted for by the notion that what matters for learning is the predictive value of a CS relative to that of other potential CSs in the situation (see Chapter 4). Here the light always predicts the US for the uncorrelated group, regardless of which tone is present. For the correlated group, T1 predicts the US perfectly and the light is irrelevant.

The tendency to learn most about the best predictors has ecological implications. Dukas and Waser (1994) exposed bumblebees (*Bombus flavifros*) to patches of artificial flowers, each decorated with two colors. For example, a bee might find yellow + blue, yellow + purple, white + blue, and white + purple flowers. Bees for which a single

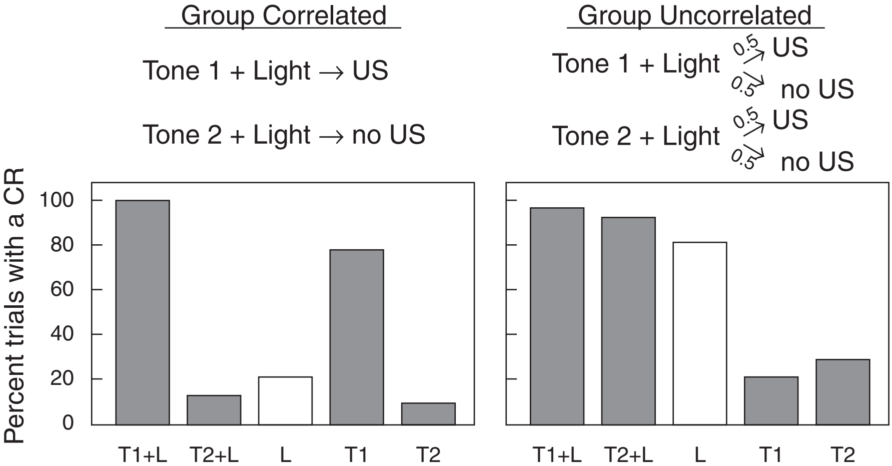


Figure 6.7. Method and results of the relative validity experiment of Wagner et al. (1968).

color reliably predicted nectar (e.g., only white + blue and white + purple rewarded) gradually increased the proportion of visits they made to rewarded flowers, but those for which no single color was a reliable predictor (e.g., only white + blue and yellow + purple rewarded) did not improve their foraging efficiency in over 300 visits. Bumblebees in the latter group would have had to learn the significance of each configuration of colors, a solution to discrimination training discussed next.

Compounds as configurations

Suppose stimulus A is reinforced and stimulus B is reinforced, but their compound, stimulus AB, is not reinforced. According to the Rescorla-Wagner model (Chapter 4) it is impossible for animals to learn to respond to A and to B but not to AB. The AB compound should support more responding than either A or B alone, not less. Nevertheless, rats and pigeons can learn such a configural discrimination. To explain how they do, elemental theories have to assume that the compound, AB, contains an extra, configural, element. In effect this corresponds to the animal's knowledge that AB is a distinct entity more than the sum of its parts. In this way the separately reinforced A and B can still be excitatory but the hypothetical configural element can gain enough inhibitory strength to cancel their combined effects.

In contrast to this approach, Pearce's (1994a, 1994b) configural theory mentioned in Chapter 4 suggests that a compound is treated as a unique stimulus, albeit one with some similarity to both A and B. Generalization between the compound and its elements makes the configural discrimination difficult, but not impossible. To account for behavior in this particular discrimination problem, there is not much to choose between configural and elemental models. Pearce's theory provides a better account of performance in some more complex discriminations involving three or four elements in different combinations, but on the other hand, there are some situations for which an elemental account does a better job (review in J. A. Harris 2006). Each account may be correct for some subset of discrimination learning situations (Pearce and Bouton 2001). Or perhaps some new model will provide a better account than any existing one (cf. J. A. Harris 2006). But both elemental and configural approaches suffer from vagueness in the specification of similarity. How do we identify the "elements" that two stimuli may or may not have in common or quantify the similarity between two compounds with common features (Fetterman 1996; D. S. Blough 2001)?

6.4.2 Generalization and peak shift

No stimulus is exactly the same twice. A red belly may be on a small or a large male or seen at different angles and distances, but it is still a sign of a male in breeding condition. If nothing else, the internal state of the perceiver or the orientation of its receptors changes from one encounter with an object to the next. *Generalization* from one thing to others that are physically similar to it makes it possible to behave consistently to events that are the same in consequential ways. The experience of eating a particular seed or butterfly is a good indication of what will follow from eating other seeds or butterflies of the same kind, so there is a sense in which the universal tendency to generalize expresses a creature's estimate that a new thing is the same kind as a thing previously learned about (Shepard 1987, 1994). As this functional account implies, generalization is seen with all sorts of discriminative behavior, whether trained in the laboratory or not (Ghirlanda and Enquist 2003). Generalizing from one thing to another does not necessarily mean the animal cannot tell them apart. In nature, there is a tradeoff between generalizing and discriminating (McLaren 1994). For instance, fear responses are likely to generalize widely because the cost of ignoring the slightest sign of a predator is likely to be greater than the cost of making a startle response to a falling leaf. Reflecting such functional tradeoffs, the extent of generalization may depend on the behavior system and the strength of motivation underlying responding.

Learned behaviors seldom generalize completely, even when they might be expected to. For example, suppose a pigeon is reinforced intermittently when a pecking key is lighted with green light but not when the key is dark. If it receives food intermittently, perhaps on a *variable interval (VI) schedule,* it will peck steadily whenever the light is on. (On a VI schedule, food can be earned with a specified average frequency but at intervals varying from very short to very long.) All it has to learn is a discrimination between light on and light off, but when the wavelength of the light is now varied, the pigeon's pecking rate will vary in an orderly way with wavelength (Figure 6.8).

After discrimination training, generalization may be tested along a dimension shared by S+ and S-. In the example above, suppose the pigeon is reinforced for pecking when the key is illuminated with one wavelength and not reinforced, or reinforced less often, for pecking at another wavelength. Now testing with stimuli varying in wavelength will reveal the highest rates of pecking not to the reinforced wavelength but to one displaced away from the unreinforced wavelength (Figure 6.8). This is *peak shift,* found with many species and stimulus dimensions (Ghirlanda and Enquist 2003; Lynn, Cnaani, and Papaj 2005; ten Cate and Rowe 2007; but see Spetch and Cheng 1998). Peak shift is generally more marked the closer together are the positive (S+) and negative (S-) stimuli (but see Baddeley, Osorio, and Jones 2007). Notice that in Figure 6.8 training a wavelength discrimination increased the rate of pecking to S+ compared to what it was in the simple discrimination between light on and light off. This increase in rate is related to the phenomenon of *behavioral contrast:* behavior in the presence of a stimulus correlated with an unchanging schedule of reinforcement depends on the reinforcement rate during other stimuli that may be present. If more frequent reinforcement is sometimes available,

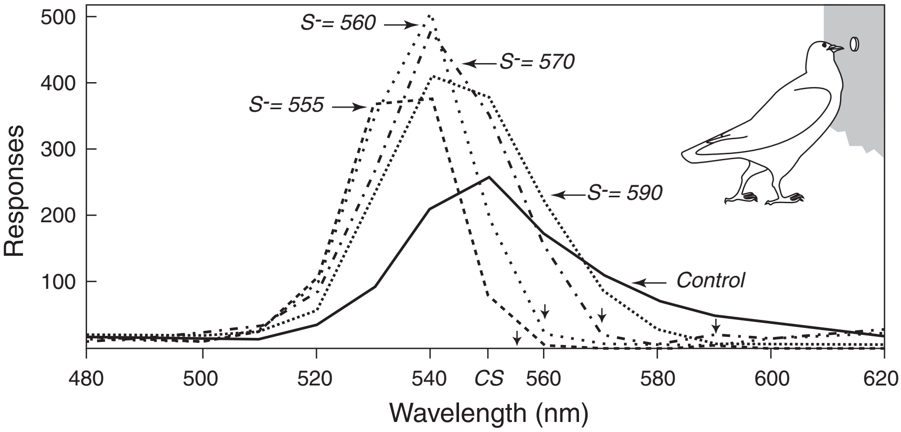


Figure 6.8. Wavelength generalization and peak shift in pigeons. The control group was simply reinforced for pecking at a key illuminated by 550 nm (CS). The other four groups were reinforced at this wavelength and extinguished at one other, S-, wavelength as indicated. Redrawn from Hanson (1959) with permission.

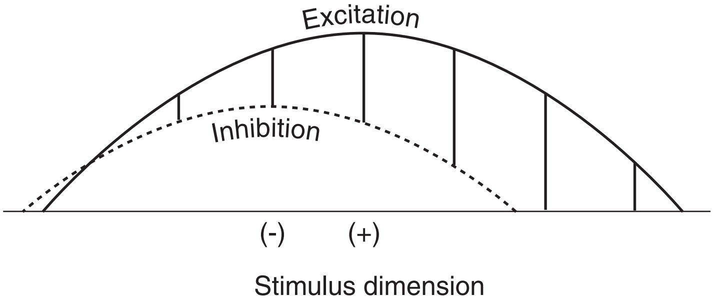


Figure 6.9. How additive gradients of excitation and inhibition can generate peak shift. The net excitation from reinforcement at S+ minus inhibition from extinction at S- is represented by the length of the vertical lines. The longest such line is not at S+ but to its right. Redrawn from Spence (1937) with permission.

responding in the constant schedule will be lower than when that schedule is contrasted with lower reinforcement rates, as if an unchanging schedule is evaluated relative to other current options.

Gradients of excitation and inhibition

From the time of Pavlov, theories of discrimination learning have been based on the notion that reinforcement results in excitatory connections between stimuli or responses and reinforcers, whereas nonreinforcement results in inhibitory ones. This notion provides a simple mechanistic account of peak shift if we assume that both excitation and inhibition generalize and that behavior toward a stimulus reflects its net excitation (i.e., excitation minus inhibition), as shown in Figure 6.9. This model, the classic Hull-Spence model, takes generalization for granted rather than trying to explain it from first principles. An alternative (Blough 1975) provides a possible mechanism for generalization by viewing the S+ and S- as each consisting of a number of elements separately associated with the US, as in the model of perceptual learning in Chapter 5. If elements individually acquire associative strength, it follows that discriminations will be learned more slowly between similar than between dissimilar stimuli. Elements common to S+ and S- will alternately gain and lose associative strength, retarding the emergence of a difference in net associative strength between S+ and S-, the more so the more common elements there are. Table 6.1 shows how this approach accounts for peak shift.

Table 6.1 An elementalist analysis of peak shift

Stimuli	1	2	3 (S+)	4 (S-)
Elements	0 1 1 2	1 2 2 3	2 3 3 4	3 4 4 5
+	+	+ + +	+ + + +	+ + +
-		-	- - -	- - - -
Net =/-	+1	+2	+1	-1

Stimuli 1–4 are composed of various proportions of elements 1–5, as indicated. If 3 is the positive stimulus in discrimination training and 4 is the negative stimulus, stimulus 2 will acquire greater net positive strength than stimulus 3. After Mackintosh (1995), reproduced with permission.

Because *inhibition* implies suppression below a "zero" level, it cannot be distinguished from absence of excitation without a moderate baseline level of behavior. One solution to this problem is a *summation test:* compound the putative inhibitory stimulus with an excitor to test whether it reduces responding more than does an untrained stimulus (Rescorla 1969). Another is to test whether excitation is acquired more slowly to the supposed inhibitor than to a neutral stimulus (the *retardation test;* Rescorla, 1969*)*. Blough (1975) conducted a summation test in which a whole range of stimuli were reinforced at a low level to generate a stable baseline of behavior. Pigeons pecked a key with a single colored line on it which could be illuminated by any of 25 wavelengths (Figure 6.10). Each time the key lit up, pecking produced food on a fixed-interval (FI) 20-second schedule; that is, when 20 seconds had elapsed since the beginning of the trial, the next peck would be reinforced. In general, food was only given on about 10% of the trials, but pecking was maintained by presenting a gray square sometimes paired with food (*a secondary reinforcer*) at the end of every trial. This procedure resulted in an increasing rate of pecking with the time a stimulus was on and similar average rates to all 25 stimuli. Generalization of excitation was studied on this baseline by giving extra reinforced presentations of a selected wavelength to increase its excitation. Similarly, inhibitory gradients resulted from extra nonreinforced presentations of a selected wavelength. Because intermittent reinforcement was continued at the other wavelengths, this procedure permitted prolonged assessment of generalization.

The sharpness of the gradient obtained in this procedure depends on when it is measured during the 20-second fixed interval (see Figure 6.10). Early in the interval responding is at its most selective. The pecking rates to all wavelengths increase throughout the interval so the excitatory gradient is nearly flat near the time of reinforcement. No other evidence is needed that generalization reflects more than lack of ability to discriminate. Here one might say that the more there is to gain from responding, as at the end of the FI, the more responding generalizes. An interesting feature of the gradients in Figure 6.10 is the "shoulders" in the inhibitory gradients on either side of the nonreinforced value. They can be generated by the elemental model in a similar way to the enhanced responding that accompanies peak shift (see Blough 2001).

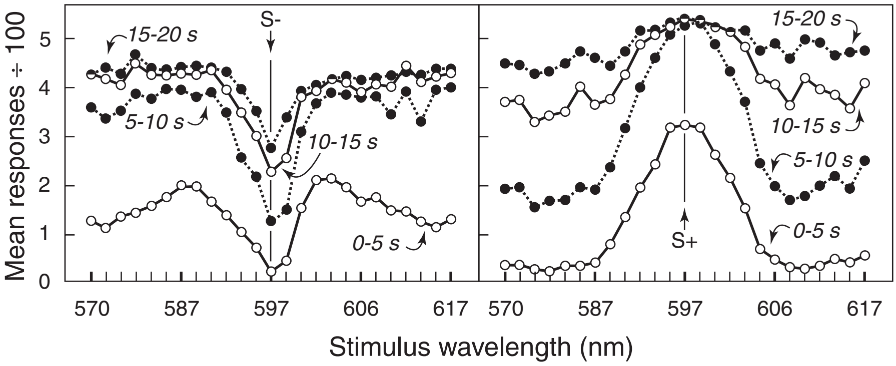


Figure 6.10. One pigeon's excitatory and inhibitory wavelength generalization gradients in Blough's (1975) experiment. Separate gradients are shown for each 5-second period of the 20-second stimulus, timed up from zero with food at the end of 20 seconds. Redrawn from Blough (1975) with permission.

Supernormality and peak shift

Peak shift is like supernormality in untrained discriminations in that stimuli with more extreme values than those normally present evoke the most responding. This similarity has stimulated discussions about possible mechanistic and/or functional commonalities between the two phenomena (Cheng 2002; Ghirlanda and Enquist 2003; Lynn, Cnaani, and Papaj 2005). The examples of supernormality described in Section 6.2.2, however, seem to differ from peak shift as depicted in Figures 6.8–6.10 in being open-ended. That is, a wide range of stimuli with characteristics more extreme than normal evoke greater responding than normal. Such responses might be the outcome of natural selection against responding to values below some criterion, for instance, objects too small to be eggs (Staddon 1975; Baerends 1982). But this is not the whole story. An important difference between features such as wavelength, in the examples in Figures 6.8 and 6.10, and features such as size and number is that the latter vary in intensity. Unlike the case with wavelength or orientation, changing an object along an intensity dimension means there is more or less of it, and even in generalization tests with explicitly trained responses, the shape of the gradient can vary with the type of continuum tested (Ghirlanda and Enquist 2003). Peak shift in any kind of discrimination may be the outcome of the kind of decision process depicted in signal detection theory (Chapter 3 and Lynn, Cnaani, and Papaj 2005). With overlapping sensory effects of two sets of stimuli such as S+ and S- (or eggs and not-eggs), the animal can be more certain that the stimulus is S+ when it differs more from S- than usual. One intriguing suggestion is that 'difference' is judged relative to the original discrimination. A small difference is more relevant after training on a difficult discrimination (Baddeley, Osorio, and Jones 2007).

6.4.3 Other processes in discrimination learning

In the wild animals must be learning new discriminations all the time. For instance, as the seasons progress and new seeds and insects appear, a young bird may need to learn how to discriminate them from the substrate, where they are most abundant, and how to handle them. Birds that migrate have to learn about new food items at stopovers along the way and in their final wintering grounds (Mettke-Hofmann and Gwinner 2003). Long-lived animals may have to learn new things about neighbors and territories in each breeding season. One might therefore wonder whether discrimination learning becomes easier with experience. That is, do animals "learn to learn"? This amounts to asking whether animals acquire anything during discrimination training besides excitatory and inhibitory connections to specific positive and negative stimuli. This question has been investigated in a number of ways (see Mackintosh 1974), but here we focus on discrimination reversal learning and learning sets. Studies of these phenomena have also yielded some noteworthy comparative data.

Serial reversal learning

Discrimination reversal learning is just what it says: after being exposed to a given S+ and S- for a number of trials an animal is now exposed to the same stimuli with their significance reversed. So if black was initially positive in a black-white discrimination, black becomes negative. In *serial reversals* the animal is exposed to a series

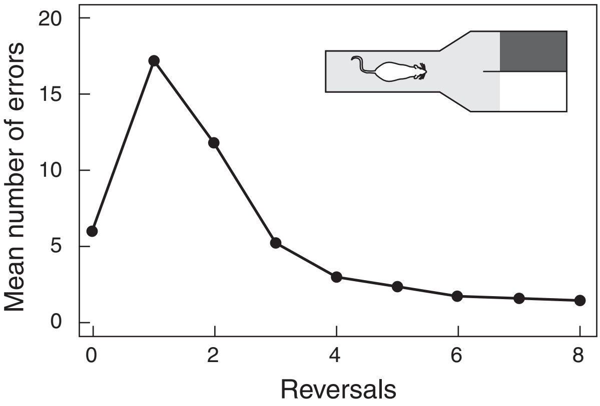


Figure 6.11. Mean total errors before making 18 correct choices out of 20 for rats trained on serial reversal of a black-white discrimination in a choice apparatus like that shown. After Mackintosh et al. (1968) with permission.

of reversals. The significance of the stimuli may change at the beginning of each experimental session. Rats typically perform worse in the first few reversals of a given problem, but they eventually perform better than they did on the first discrimination (Figure 6.11). Optimal performance is one error per reversal. This can be attained by adopting a *win stay—lose shift* strategy: always try the response that was last rewarded, and if that is no longer rewarded, shift to the other response, otherwise stay. Monkeys seem to learn this strategy, but rats do not. Instead, two other things seem to happen. First, a long series of daily reversals causes *proactive interference* (*PI,* see Chapter 7) in memory. The rat has had so many reversals that it cannot remember at the beginning of one day which response was rewarded yesterday, so it performs at chance. (At the beginning of each early reversal, performance is below chance; at this stage the rat evidently does remember the last problem.) Second, performance increases from 50% correct, or chance, more quickly in late than early reversals, suggesting that rats gradually learn what stimuli to pay attention to in the experimental situation.

Rumbaugh and his colleagues (Rumbaugh and Pate 1984; Rumbaugh, Savage-Rumbaugh, and Washburn 1996) compared primates on a version of reversal learning in which animals were first trained to a criterion of either 67% or 84% correct with a given pair of objects and then given ten trials with the significance of the objects reversed. This procedure was repeated with a series of new pairs of objects. An animal influenced only by past reinforcement with given objects should reverse more slowly the higher the original criterion, whereas one that has learned the principle of reversal might be expected to do just the opposite because the better it knows the current contingencies the easier it should be to tell when they reverse. In a comparison of 13 primate species, most of the prosimians tested showed the former pattern, the apes showed the latter, and the monkeys were intermediate (Rumbaugh, Savage-Rumbaugh, and Washburn 1996).

Some common tasks for studying children's cognitive development essentially require reversal learning. For example, in Piaget's classic test of object permanence, the child sees an object hidden in one place, A, and successfully retrieves it. But when the same object is now hidden in another place, B, a very young child will continue reaching for it in A, failing to reverse the previously successful response. But even while committing this *A not B error* in responding, the child may be looking toward B, as if knowing where the object is but being unable to inhibit the old behavior. The disappearance of this error somewhere between the ages of 1 and 2 years is but one of many kinds of evidence for the growth of inhibitory control during human development. Indeed, the same trend, along with evidence for its link to development of the prefrontal cortex may be seen in non-human primates (Hauser 2003). Differences in reversal learning among primates such as those reported by Rumbaugh and colleagues could be related to species differences in this area of the brain.

Learning set

Tests for *learning set* are like discrimination reversals in that the animal is trained on many discrimination problems in succession, but the stimuli are different in each problem. As in reversal learning, general factors like learning to ignore irrelevant cues can improve performance over problems. The optimal strategy for learning set is again win stay—lose shift because an animal can do no better than choose randomly on the first trial of each problem and then stay with the alternative chosen first if it was rewarded, otherwise shift. Proportion correct choices on the second trial is a measure of the extent to which this strategy has been acquired. The ability to acquire a learning set has been used to compare animals in "intelligence." This is an appealing kind of test because "learning to learn" does seem intelligent from an anthropocentric point of view. In addition, the shape of the curve representing number of errors as a function of successive problems seems to be a meaningful measure of learning regardless of its absolute level. Whether individuals of a particular species learn the first problems slowly or quickly, one can still ask whether they improve over problems and whether they eventually attain the optimum of perfect performance on the second trial of each new discrimination.

The view that learning set is a good test of animal intelligence was encouraged by early data from mammals (Figure 6.12). The ordering of species, with rhesus monkeys performing better than New World squirrel monkeys, which performed better than cats, and rats and squirrels doing worst, is consistent with the assumption that animals can be ordered on a single ladder of intellectual improvement. However, this naive interpretation (see Chapter 2) is not even supported by further data on learning set. Data of other mammals do not fall where they would be expected to (Macphail 1982), and at least one bird species, blue jays, acquire a win stay/lose shift strategy like rhesus monkeys do (review in Kamil 1985). In both blue jays and monkeys, staying or shifting depends—as it would be expected to—on memory for the first trial of a problem. Accuracy on the second trial of a new discrimination falls as the time between trials (the *inter trial interval* or *ITI*) lengthens so that the outcome of the first trial is forgotten.

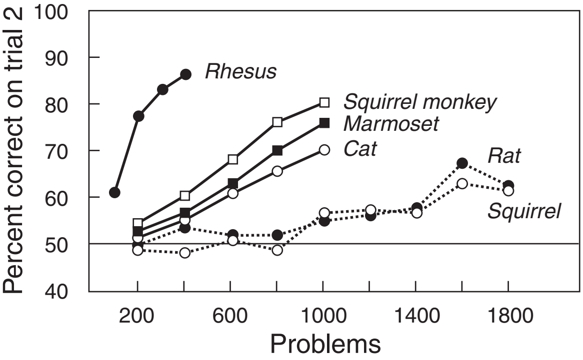


Figure 6.12. Visual discrimination learning set performance of six mammalian species, redrawn from Warren (1965) with permission.

The results of learning set experiments with rats deal a further blow to the idea that learning set performance is a unitary reflection of a species' "intelligence": the sensory modality of the stimuli to be discriminated has an overwhelming effect on rats' performance. The rat data in Figure 6.12 come from an experiment with visual stimuli: in over 1000 problems, the rats' accuracy on second choices hardly rose above chance. But with spatial cues rats acquire a learning set within fewer than 50 problems (Zeldin and Olton 1986), and with olfactory cues they do so even faster (Eichenbaum, Fagan and Cohen 1986; Slotnick, Hanford, and Hodos 2000). The many procedural differences among experiments with different cues could have contributed to the differences in results, but they are consistent with evidence that rats have excellent memory for olfactory and spatial cues (Chapter 7).

Attention

In the Rescorla-Wagner model (Chapter 4), the learning rate parameter α is a measure of the salience of a CS. Salience is assumed to be determined by physical features of the CS—for instance a dim light has lower salience than a bright light—and by the animal's species-specific sensory abilities. For instance, odors are probably more salient than colors for rats, while the reverse is likely true for most birds. But some elaborations of the Rescorla-Wagner model have assumed that in addition associability or salience of stimuli, α in the equation for learning, can change with experience (for a review see Pearce and Bouton 2001). Intuitively, it might seem that as a stimulus acquires predictive value it would be attended to more: good predictors deserve more attention, so α should increase as associative strength increases (Mackintosh 1973). But it is equally plausible that well-learned predictors are responded to automatically, so α of a CS should decrease as its associative strength increases (Pearce and Hall 1980). There is some evidence consistent with each of these views, suggesting that each one is correct in some yet-to-be-specified circumstances.

Experience may change attention not just to particular stimuli but to whole stimulus dimensions or modalities. For example, Blough (1969) reinforced pigeons intermittently for pecking in the presence of a single combination of tone frequency and wavelength out of 49 such compounds made up of 7 tones and 7 wavelengths. The birds could perform well only by paying attention to both tone and light. That they did so was shown by steep generalization gradients along both tone frequency and wavelength (Figure 6.13). But when one feature of the reinforced stimulus was made irrelevant by keeping it constant for several sessions, the gradient along that dimension flattened dramatically, indicating that the birds were paying less attention to it.

Several other sorts of data have also been thought to point to changes in attention during discrimination training (Mackintosh 1974, 1983). For instance, performance on a color discrimination is better following previous training on another color discrimination than following training on, say, an orientation discrimination. In such experiments, possible effects of simple stimulus generalization from one discrimination to the next need to be ruled out by varying the positive and negative stimuli for different animals and by making them as dissimilar as possible from one discrimination to the next. If an animal trained with red positive and green negative showed positive transfer to a discrimination with orange positive and blue negative, an appeal to stimulus generalization would be more appropriate than an appeal to increased attention to wavelength. Despite the intuitive appeal of

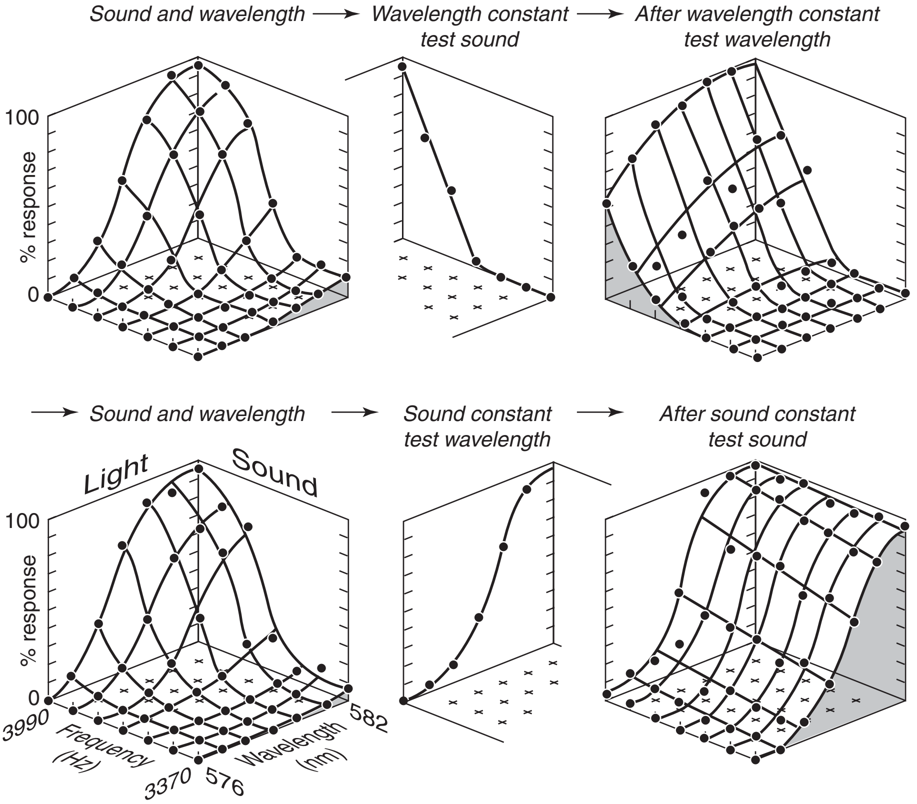


Figure 6.13. Generalization along the dimensions of wavelength and sound frequency following reinforcement at a single combination of wavelength and frequency. A single pigeons' rate of pecking is shown as proportion of rate to the reinforced wavelength and tone frequency. After Blough (1969) with permission.

the notion that animals learn what to pay attention to, it has proven remarkably difficult to obtain unambiguous evidence for changes in attention in conventional discrimination learning because of the difficulty of ruling out such specific transfer effects (Mackintosh 1983). Procedures like Blough's together with tests of short-term memory have been more illuminating (Riley and Leith 1976; see Chapter 7). Nevertheless, this does not mean that animals do not learn what to attend to in discrimination learning experiments. The ability to acquire new discriminations does improve with experience, probably for a variety of reasons. The processes involved may be important in variable environments in nature.

6.5 Category discrimination and concepts

Example 3 at the beginning of this chapter depicts a classic series of experiments (Herrnstein, Loveland, and Cable 1976; Herrnstein 1979) in which pigeons were trained to classify photographic slides according to their membership in categories such as "tree" and "non-tree." Typically, birds were trained with about 40 S+ slides, all having exemplars of the category, and 40 S- slides, lacking exemplars. The slides were presented in random order on a multiple schedule, so that each one was on for a minute or so. A bird was reinforced intermittently for pecking at S+ slides and not reinforced for pecking at S- slides. A correction procedure might be used in which each negative slide remained on until a certain number of seconds had elapsed without pecks, thus extending the period of extinction for poorly learned negative slides. The data consisted of response rates before the first reinforcer in positive slides and during a comparable period for negative slides. In general, pigeons learn remarkably quickly with such a procedure to classify photographs representing a large number of human-defined natural categories including water, fish, and people as well as trees (see Chapters 16–21 in Wasserman and Zentall 2006b; Zentall et al. 2008). Most importantly, they generalize to new instances. For example, birds that respond at a higher rate to trees than to non-trees continue to do so when shown slides they have never seen before (Herrnstein 1979).

This research attracted attention because the results seem to suggest that the birds "have a concept" in the same way humans do. Indeed, one of the first articles about it (Herrnstein, Loveland, and Cable 1976) was titled "Natural concepts in pigeons." However, what animals are doing in such experiments is best referred to operationally, as *category discrimination*. That is, they are behaving differently to different categories of items. One can then ask whether any special processes underlie this behavior. Besides possibly illuminating mechanisms of human performance in comparable situations (Mackintosh 2000; Ashby and Maddox 2005), the results are of interest from an ecological point of view because objects to be discriminated in nature are, like the slides in Herrnstein's experiments, more complex and variable than the stimuli typical of traditional discrimination learning experiments.

The pigeons in Herrnstein's experiment are discriminating on the basis of membership in a *perceptual category,* as distinct from a *functional category*. The former is defined by perceptual features of its members, whereas the latter is defined by some other property such as being edible or being related to a dominant female. For example, screwdrivers belong in a perceptual category of *long thin objects* along with pencils and carrots, but they also belong in the functional category *tools* along with hammers and saws. In effect, all members of a functional category have a common associate, for example, edibility or Female A as a relative. Categories may also be *relational;* that is, a set of two or more things belongs to the category if it instantiates a specified relationship such as identity or mother and offspring.

As may be apparent, much psychological research on animal category learning is decidedly anthropocentric (Zentall *et al.* 2008). The key question is what representational ability is implied by performance such that of Herrnstein's pigeons. We will see that perceptual or functional category learning requires no more than the species-general ability to associate surface features of stimuli with reward and/or with one another; no special ability for abstraction or conceptualization need be invoked. When it comes to relational categories, however, in particular same versus different, it's another story. Although both primates and pigeons can be trained, sometimes with great difficulty, to categorize displays as to whether the items in them are all the same or not, they seem to do so on the basis of perceptual variability. This makes their performance very different from that of people, most of whom classify such displays categorically—either the same or different, not more or less variable (Castro, Young, and Wasserman 2006)—and who possess a domain general concept of sameness. That is, people can represent second-order relationships, those abstracted from the first-order or perceptual features of stimuli. This sensitivity has been suggested to characterize a pervasive mental discontinuity between humans and all other species (see Chapter 15; Penn, Holyoak, and Povinelli 2008).

6.5.1 Perceptual category discrimination: Memorizing and generalizing

When photographs of real-world scenes and objects are the stimuli in a category discrimination experiment, animals do not have to see them as representing real things in order to classify them correctly. Indeed, it is questionable whether pigeons see the photographs in experiments like Herrnstein's as anything other than arrays of colored blobs (Box 6.1). Monkeys trained to discriminate slides with people from those without people proved to be responding partly to red patches: slides showing a slice of watermelon or a hyena carrying a dead flamingo were treated like slides of people (D'Amato and Van Sant 1988). Thus learning perceptual category discriminations may have little to do with human-like conceptual representations of the things depicted. Rather, much of what is going on can be accounted for as simple discrimination learning and stimulus generalization.

Because memorizing 80 or more individual slides seems quite a feat, the possibility that pigeons solve category discriminations by doing so was initially discounted. However, it turns out that pigeons can memorize many more than 80 slides. Vaughan and Greene (1984) trained birds with a total of 160 S+ and 160 S- slides. This was a *pseudocategory* discrimination: slides were assigned to the positive and negative sets regardless of perceptual similarity or natural category membership. Nevertheless, within a few sessions with each new set of 40 positive and 40 negative slides appearing twice per session, the birds were pecking more to most positives than to most negatives. Moreover, they still performed the final discrimination with 320 slides well above chance after a rest of more than two years. Pigeons trained similarly for 2 to 3 years with an ever-increasing pool of pictures were estimated to remember over 800 individual slides (Cook et al. 2005).

Pigeons are also sensitive to fine details like those differentiating one photograph of a scene from another taken a few minutes later (S. Greene 1983). But memorization is not the whole story. Pigeons generally learn faster and perform better with categorical groupings than with pseudocategories (S. Watanabe, Lea, and Dittrich 1993). But members of a perceptual category like "tree" or "fish" have more in common as visual stimuli (e.g., patches of green, certain kinds of contours) than members of a random collection of things. Thus stimulus generalization among category members will tend to improve performance with categories while, if anything, the same process will impede learning of pseudocategories.

The earliest experiments on category discrimination consisted largely of demonstrations that pigeons and a few other species could learn most—though apparently not all—category discriminations (S. Watanabe, Lea, and Dittrich 1993). However, to understand what such performance is based on, a more analytical approach was needed. Wasserman and his colleagues (review in Wasserman and Astley 1994) pursued such an approach by, in effect, asking pigeons, "What category does this slide belong to?" and giving them four possible answers. This is like the "name game," in which an adult shows pictures to a young child and asks, "What is it?" The pigeon viewed a central slide representing a member of one of four categories, for example cats, flowers, cars and chairs (Figure 6.14). After being required to peck at the slide a number of times, ensuring that it was processed, the bird chose among four keys, one at each corner of the viewing screen. A peck at the upper right, red, key might be reinforced if the slide showed a cat, a peck at the lower left, green, key, reinforced if

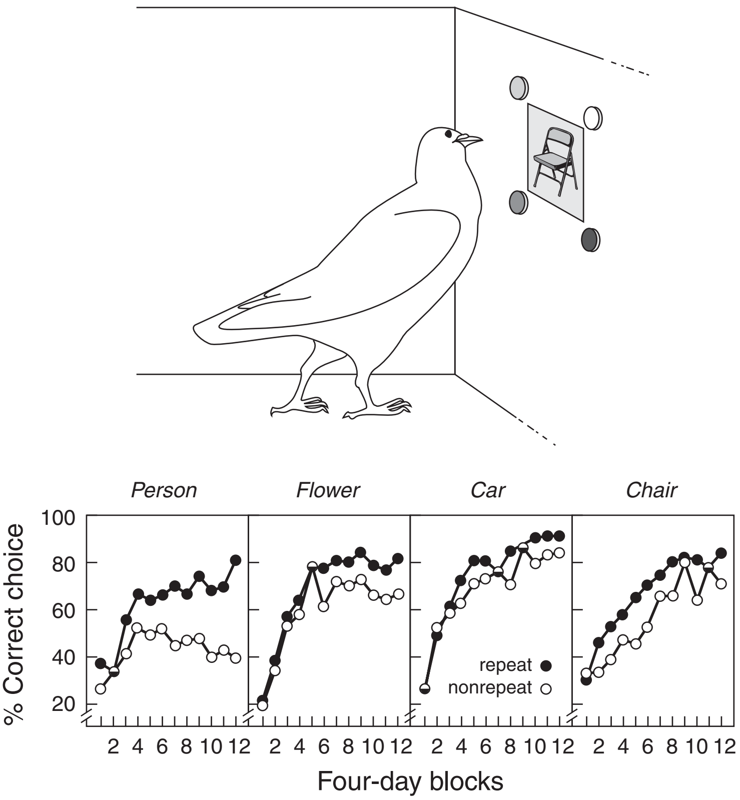


Figure 6.14. Apparatus for training four-way categorization in pigeons and performance on slides never seen before (nonrepeat) compared to performance on slides repeated from session to session. Data redrawn from Bhatt et al. (1988) with permission.

the slide showed a car, and so on. With 10 instances of each category, pigeons chose correctly about 80% of the time within 10 days of training, seeing each slide just once a day (note that chance performance is only 25% correct).

This procedure was used in a series of experiments which documented how pigeons' discrimination among categories of photographs is based on a combination of memorizing exemplars and generalizing from them. For instance, when the number of training slides per category was varied from 1 (i.e., a discrimination among only four slides) to 12, pigeons learned more slowly the more slides per category, consistent with a role for memorizing individual slides. On the other hand, when tested with new slides after reaching 70% correct on training slides, they performed better the more exemplars of each category they were trained with. This result should not be surprising. The more, say, cat slides the bird has been exposed to, the more likely a new cat slide will be similar to one seen before. Perhaps the best evidence for the joint contribution of memory and stimulus generalization was an experiment in which pigeons were able to learn a category discrimination even though each slide was shown only once (Figure 6.14). The birds evidently learned enough from a single trial with each slide to permit generalization to new slides of the same category. This could mean that only the common features of each category were learned, since these would be repeated from exemplar to exemplar. However, when novel slides were intermixed with slides being shown for the second time, performance was worse on novel than on familiar slides. Thus, the birds apparently memorized features or combinations of features unique to single slides as well as features common to many slides. Pigeons can also learn to classify a given set of images in two ways concurrently (Lazareva, Freiburger, and Wasserman 2004), a laboratory analogue of the multiple classification of social companions described in Chapter 12.

6.5.2 The contents of perceptual category learning: Exemplars, features, or prototypes?

What has an animal learned when it can accurately classify stimuli into perceptual categories? One answer was suggested in the preceding section: the animal simply learns the characteristics of every slide as a whole (Wasserman and Astley 1994; Chase and Heinemann 2001). Associative strength is acquired to each individual stimulus, and by definition there is more stimulus generalization within than between perceptual categories. However, a theory based on learning of elements makes similar predictions to exemplar learning here. The elemental approach starts from the observation that perceptual category membership is defined by the possession of certain features. For instance, trees are likely to be green, have leaves and/or branches, dark vertical trunks, be outdoors, and so on. But obviously many nontrees—for instance celery stalks—have one or more of these features, too. Furthermore, natural categories may be *polymorphous;* that is, not all category members have all the same features, although each has at least a subset of them. For instance, birch trees have a trunk and leafy branches with white bark, pine trees have a trunk with dark-colored bark but needles in place of leaves. An elemental analysis of categories proposes that nevertheless a set of features can be found such that the conjunction of some number of them separates category members from other things. The number and identity of conjoined features may vary from instance to instance, as with trees.

A more analytical approach than using collections of photographs is to create categories of artificial stimuli (Figure 6.15). Reinforcement for responding to each feature can depend on the other features with which it appears, much as with objects forming natural categories (e.g., in a tree–no tree discrimination, a leafy oak tree is positive, but a leafy celery stalk, negative). Pigeons can learn category discriminations with stimuli like those depicted in Figure 6.15 (Huber and Lenz 1993; Lea, Lohmann, and Ryan 1993; Huber and Lenz 1996), but they do not always learn as quickly as they learn to categorize colored slides of natural scenes. One reason may be that, unlike the case with natural categories, the artificial categories have been designed so that no one feature or cluster of features is more predictive of category membership than others. For instance, each artificial seed in Figure 6.15 is described by values of each of five features (spotted/plain, fat/thin, stripe curved/straight, horizontal/vertical, rounded/pointed). Because category membership depends on any three or more features being shared with the perfect exemplar, each feature is equally important. In contrast, in many natural categorization problems such as that depicted in Figure 6.4 some features predict category membership better than others.

Huber and colleagues (Huber and Aust 2006) analyzed something more like a natural categorization problem with controlled stimuli by using computer-manipulated images of human faces. Like other research summarized below, this work supports the conclusion that pigeons use both elements and configurations of elements, depending on the task. An even more stripped-down and well-controlled approach to creating

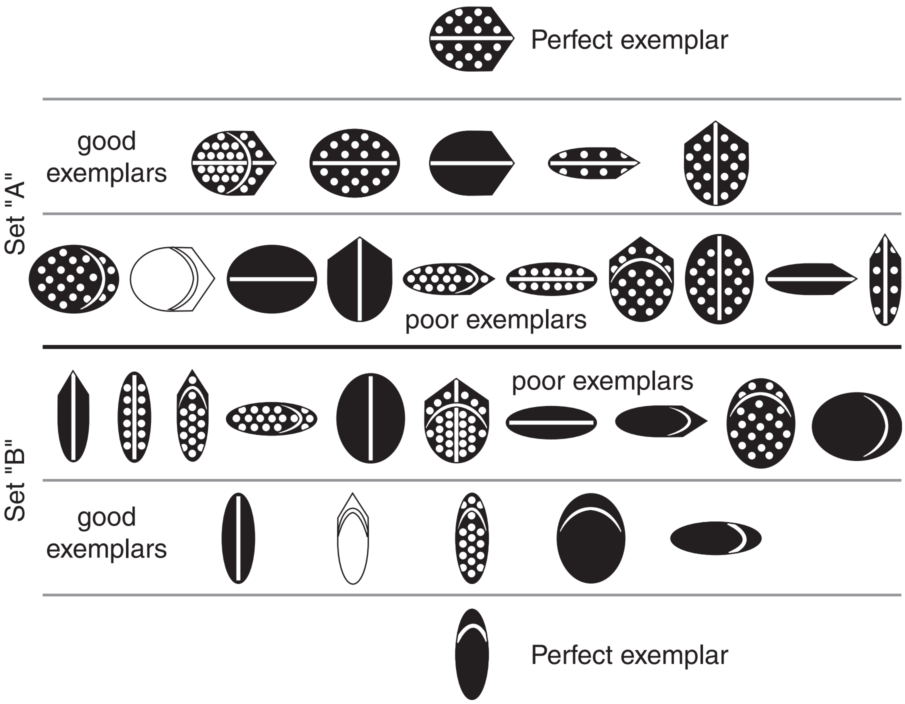


Figure 6.15. "Artificial seeds" for category discrimination experiments. The perfect exemplar of Set A is fat, dotted, horizontal, with a straight stripe present and a curved stripe absent. The perfect exemplar of set B has the opposite value of each of the five features. "Good" and "poor" exemplars have only 4 or 3 features, respectively, in common with the perfect exemplar of their category. Redrawn from Lea, Lohmann, and Ryan (1993) with permission.

naturalistic categories is to create overlapping sets of stimuli that vary continuously along two dimensions, such as height and width (Shimp et al. 2006). Just as in the stimulus space defining songs from two bird species (Figure 6.4), categories are defined probabilistically, with items near a central value being more likely than more deviant ones. For example, a "high wide" category might include a few "low narrow" exemplars. Reasoning familiar from signal detection theory (Chapter 3) predicts the optimal choice of the response corresponding to each category. Pigeons do choose close to optimally with a variety of categorization rules. For example, as in Figure 6.13, when the relevance of one dimension changes relative to the other, pigeons' weighting of it changes accordingly,

Both exemplar-learning and element-learning accounts of category discrimination are fundamentally associative: exposure to each instance changes associative strength of the whole exemplar or its features, respectively, and performance to other exemplars and nonexemplars is based on stimulus generalization. A somewhat different account, derived from human concept learning (Ashby and Maddox 2005), is that exposure to individual exemplars results in the formation of a representation of a category *prototype,* a sort of ideal exemplar, the central tendency of all exemplars. The prototypical bird, for instance, is more like a robin or a sparrow than a penguin or an ostrich. Categorization of exemplars is based on comparing them to the prototype.

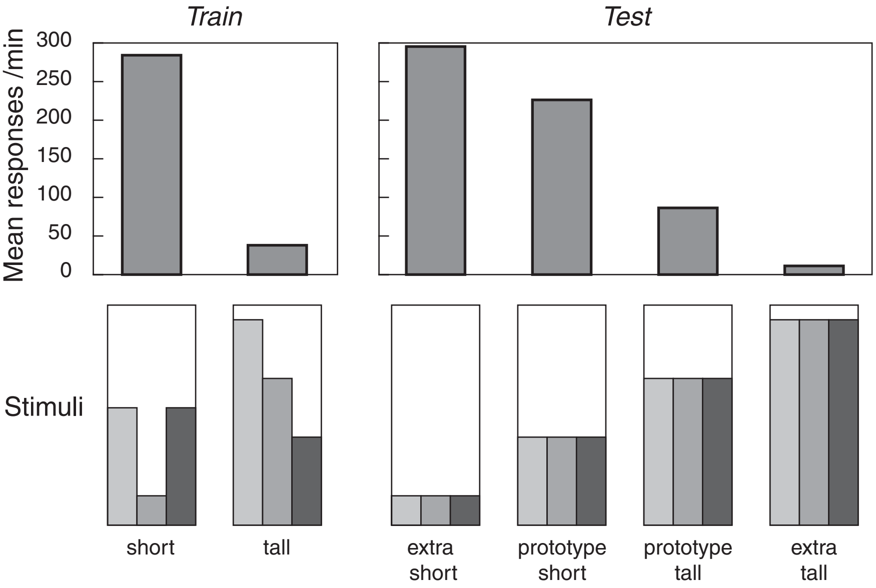


Figure 6.16. Stimuli and data from Pearce's (1989) experiments on artificial category learning by pigeons. After Pearce (1989) with permission.

Prototype theory makes two predictions that at first sight appear to be unique, but they can equally well be generated by associative theories. One prediction is that categorization of the prototype stimulus itself should be more accurate than categorization of any exemplars, even if the prototype has never been seen before. Pearce (1988, 1989) tested this prediction using categories consisting of patterns of three colored bars (Figure 6.16). Individual bars varied in height from 1 to 7 units, and patterns were classified in terms of the total height of their components. Patterns with a total of 9 units were positive; a total of 15 units defined a negative pattern. Individual bars could be 1 to 5 units high in positive patterns and 3 to 7 units high in negative patterns. Thus, some individual stimulus elements (here, bars 3, 4, or 5 units high) could appear in a pattern belonging to either category.

One would suppose that the prototypical positive pattern would be one composed of three 3-unit bars; similarly, the negative prototype is three 5-unit bars. Pearce's pigeons saw neither of these patterns in training, but they were tested with the prototypes and other novel patterns after learning the category discrimination (Figure 6.16). Response rates were not highest to the prototype "short" pattern and lowest to the "tall" one. Instead, the birds showed the most extreme response rates to extra-short and extra-tall patterns. This result can best be described as peak shift. The birds appear to have treated the individual bars as the stimulus elements, which gained excitatory or inhibitory strength as they were paired with reinforcement or nonreinforcement, respectively. Because bars 1 unit high could occur in positive but not negative patterns, they would be more strongly associated with reinforcement than bars of length 3, which could occur in both positive and negative patterns. Similarly, most inhibition would accrue to bars of length 7.

This associative, element-based account of Pearce's results implies that a *prototype effect* (best discrimination between the central tendencies or prototypes of the

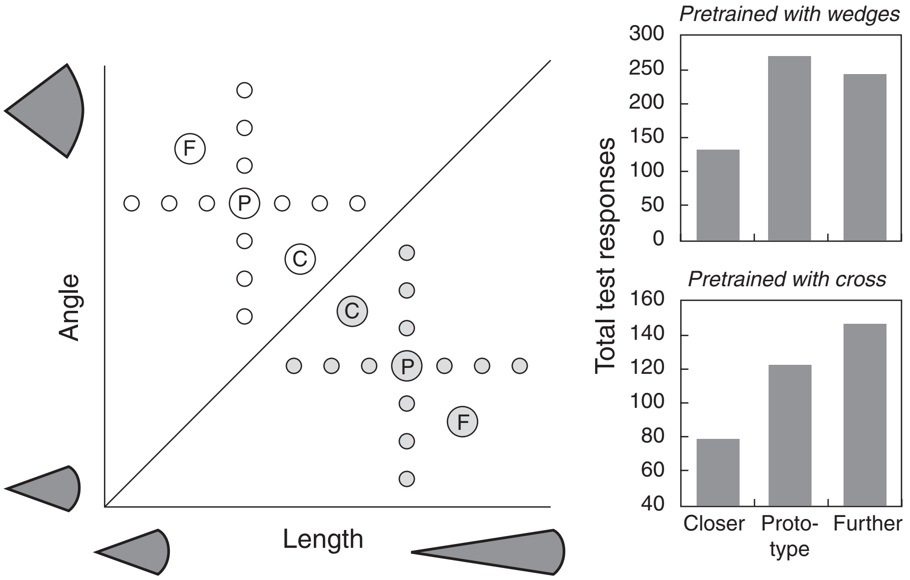


Figure 6.17. Two-dimensional space defining the stimuli used by Mackintosh (1995). Pigeons were trained in two different ways to discriminate stimuli above the diagonal line from stimuli below it. Small disks represent the stimuli used in training; larger disks, the stimuli used in testing, that is, the category prototype (P) and stimuli closer to (C) and farther from (F) the category boundary than the prototype. After Mackintosh (1995) with permission.

categories) might still be found with certain categories and training procedures. Mackintosh (1995, 2000) reported just such an effect (Figure 6.17). As in Pearce's experiment, pigeons were trained to discriminate two artificial categories without being exposed to the prototypes of those categories. Testing with new stimuli revealed a prototype effect if the birds had been trained initially to peck at all 12 stimuli that defined the positive stimulus class. By itself, this training results in greatest associative strength to the stimuli with the central values of the set, that is, the prototype. Peak shift was obtained when the birds had only pecked at a black cross before category discrimination training began.

In general *prototype* suggests a specific configuration, not just a set of features. In Pearce's experiments with the rows of colored bars, for example, the average height of the whole row defined category membership (for the experimenters, if not for the pigeons). But by designing categories of three colored bars such that no one element appeared more frequently in one category than the other, Aydin and Pearce (1994) obtained a prototype effect, which they attribute to the pigeons learning each display as a configuration. Similarly, Huber and Aust (2006) concluded that pigeons use both facial elements and their configuration to categorize simplified images of human faces. Because a combination of elements in a certain configuration is what characterizes a specific image, or category exemplar, it might appear that this is no different from an exemplar-based account. However, it differs from pure exemplar learning theory in specifying the dimensions for generalization from learned exemplars, namely elements and their spatial arrangement. A mathematical model of configural learning (Pearce 1994a) accounts for Aydin and Pearce's findings and related ones.

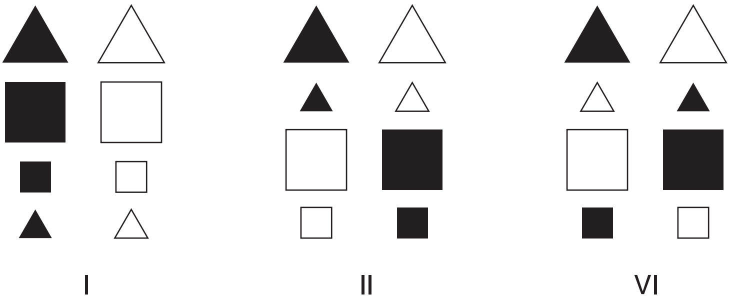


Figure 6.18. Example of three tasks used by Smith, Minda, and Washburn (2004) to compare category learning by rhesus macaques and people. In each set, one response is rewarded for stimuli on the left, the other for stimuli on the right. Both species find Task I easiest; humans find Task II intermediate and Task VI hardest. All tasks other than Task I are equally hard for macaques. Redrawn from Smith, Minda, and Washburn (2004) with permission.

The discussion so far suggests that, just as in humans (Ashby and Maddox 2005), what is learned from category discrimination training is flexible and depends to some extent on how the categories are constructed. If a difference along just one dimension defines a category boundary, animals will base responding on one element (Shimp et al. 2006), whereas if all elements are shared between categories and their configuration must be used, it will be (Aydin and Pearce 1994; Huber and Aust 2006), and if categories are defined arbitrarily, at least pigeons will memorize the significance of every exemplar. Rule-based category representations, however, may be unique to humans (J. Smith, Minda, and Washburn 2004). To take an example from a simple perceptual category, Task II in Figure 6.18, triangles and squares that are either black or white and either big or small can be classified according to the rule " "It's an A if it's a black triangle or a white square; otherwise it's a B." No single feature predicts category membership here, but this classification is easier for people to learn than more arbitrary groupings of the same stimuli in which the significance of the exemplars must be memorized separately, as in Task VI in Figure 6.18. Rhesus macaques, however, find all such tasks similarly difficult, as would be expected if they must learn all by memorizing the exemplars. However both macaques and humans, find Task I the easiest classification to learn, that is, one based on a single common element, "A's are black, B's are white' (J. Smith, Minda, and Washburn 2004). This is a nice example of how imposing different kinds of classifications on a single stimulus set can reveal species differences.

6.5.3 Functional categories and equivalence classes

Members of a functional category may be perceptually similar—consider *writing implements* for example—but they have more than perceptual attributes in common. In the laboratory, functional (or associative) categories are typically designed so the members share only an associate: a reinforced response, or a specific stimulus, reinforcer or US. We have already seen that some animals can learn such arbitrary groupings (pseudocategories) by brute-force memorization. But members of genuine functional categories are connected by their associate(s) in such a way that performance toward all category members is affected by changing the significance of one of them. The common associate serves as a common element that mediates generalization among category members. This is what Hull called *mediated* or *secondary generalization* (see Delius, Jitsumori, and Siemann 2000; Urcuioli 2006). Research using three different paradigms—and to some extent different explanatory frameworks—has shown that animals can learn functional categories and provided some information about how they do so.

Conceptual knowledge in humans links members of a category so that, for example, learning that "tools are cheap here" immediately changes our behavior toward all members of the class *tool* (Lea 1984). What this implies for animal category learning is illustrated by an experiment in which pigeons learned a pseudocategory discrimination with 40 unrelated positive slides and 40 unrelated negative slides (Vaughan 1988). When the birds were reliably pecking more to most of the positive than to most of the negative slides, their significance was reversed so the birds were now reinforced for pecking the originally negative slides and not for pecking the original positives. When the birds were once more responding appropriately, the significance of the two categories was reversed again, and so on. Finally, after 20 or more reversals, reversing the contingency with a few slides was enough to result in responding to the remaining slides that was appropriate to the new contingencies, as if all members of a category were *functionally equivalent*.

With relatively large categories of items as in Vaughan's experiment, repeated reversals are generally needed to develop functional equivalence (Delius et al. 2000). This is not true in the two other paradigms that have been used to investigate functional equivalence, perhaps because the categories involved are small. Indeed, the *many-to-one* (MTO) matching to sample procedure illustrated in Table 6.2 is essentially the minimal category learning procedure. In brief, on each trial of an MTO matching experiment, the animal first sees a *sample* stimulus and is then given the choice of two *comparison* stimuli, say X and Y. Importantly, each set of comparisons is used with two or more possible samples. For instance, choice of X is reinforced after samples A or B, choice of Y after samples C or D. To test for functional equivalence of

Table 6.2 Many to one matching and mediated conditioning as tests of acquired equivalence.

Many-to-one matching to sample					
Initial training		Reassignment		Acquired equivalence ?	
Sample	*Choice**	*Sample*	*Choice*	*Sample*	*Choice***
A	$\underline{X}$ vs. Y	A	X vs. $\underline{Y}$		
B	$\underline{X}$ vs. Y			B	X vs. $\underline{Y}$?
C	X vs. $\underline{Y}$	C	$\underline{X}$ vs. Y		
D	X vs. $\underline{Y}$			D	$\underline{X}$ vs. Y?
Mediated conditioning (Ward-Robinson and Hall 1996)					
A – grape pellets		A – shock			
B – grape pellets				panel push to B?	
C – nothing				panel push to C?	
Control group					
A – nothing		A – shock			
B – nothing				panel push to B?	
C – grape pellets				panel push to C?	

*Note: reinforced option is underlined
** No reinforcement given; underlined choice would be evidence of acquired equivalence

A with B and of C with D, training proceeds with reversed contingencies for, say, A and C. Once these are learned, if the pairs of stimuli have become equivalent in the first phase, B and D will now be responded to in a way more appropriate to the new than to the old contingencies, as indeed they are (Urcuioli 2006).

Logically equivalent procedures have been used with Pavlovian conditioning, as shown in Table 6.2 (Hall 1996). For example, in Ward-Robinson and Hall's (1999) experiment with rats, CSs A and B signaled grape-flavored food pellets for the critical group whereas C signaled nothing. In Phase 2, A was now followed by shock while B and C were not presented. The effects of this experience on evaluation of B and the control CS C were then tested by presenting B and C while the rats were pressing a panel for plain food pellets. Responding on such a baseline typically increases during a food-associated CS and decreases during a shock-associated CS. As predicted if Phase 1 training had made A and B functionally equivalent, rats panel-pressed less during B than during the neutral C, whereas the reverse was true for the control rats treated as shown in Table 6.2.

Ward-Robinson and Hall (1999) explain their results as an instance of *mediated conditioning*. In effect, at the end of Phase 1, A and B both evoke a representation of grape pellets. In Phase 2, shock occurs when this representation is activated, serving to link the grape pellet representation to shock. Then when B is presented in the test, the common association with grape pellets, now with its further link to shock, mediates reduced responding. In a more direct test of such mediated conditioning, the same rats later received grape pellets for bar pressing. The rats in the experimental group bar pressed less than those in the control group for which CS C, previously unpaired with pellets, rather than CS B had signaled shock in Phase 2. Notice that grape pellets themselves had never been paired with shock, only their representation. On the reasonable assumption that a stimulus can evoke a representation of an upcoming reinforced response (called *prospective coding* in the matching to sample literature; see Chapter 7) a similar argument explains functional equivalence in matching to sample, but it may not be the whole story (see Urcuioli 2006).

In Chapter 14 we learn that diana monkeys and some other animals show common behavior to alarm calls of their own species, alarm calls of other species, and predator vocalizations. This seems to be an example of many-to-one matching, or classification. Acoustically different signals are to some extent functionally equivalent, but whether the behavioral equivalence is mediated by a representation of a predator per se or of the response to be made to it is a matter of debate, part of a more general discussion of how animal communications have their effects (Chapter 14; Seyfarth and Cheney 2003a).

More than functional equivalence is implied by *equivalence classes,* or *Sidman equivalence,* after Murray Sidman, who first specified their characteristics on the basis of studies of verbal labeling in children. Members of an equivalence class are entirely logically equivalent, just as the word *dog,* a picture of a dog, and a real dog are in some sense equivalent. This equivalence emerges from simple experience of learning to match members of such a class to another without special additional training, making it what Sidman (e.g., 2000) calls an *emergent relation*. Members of equivalence classes satisfy tests of logical transitivity, symmetry and reflexivity as well as equivalence in the sense discussed so far. Symmetry means that having been trained to choose comparison B when A is the sample in matching to sample, without further training a subject chooses A if B is the sample. Transitivity implies that training to choose B when A is presented and C when B is presented will result in C being chosen when A is presented (and as well, A is chosen when C is presented).

And reflexivity means logically A = A. These kinds of performance emerge in language-competent children, but there is little evidence from other species—mainly pigeons—for the spontaneous emergence of the full package after training on one part of it (Jitsumori et al. 2002; Zentall, Clement, and Weaver 2003; Urcuioli 2006). An exception may be the sea lion trained extensively with a matching procedure similar to Vaughan's (Schusterman and Kastak 1998; Schusterman, Kastak, and Kastak 2003). However, just as in any cross-species comparisons, it is important to ask whether the procedures used are entirely comparable across species, and they may not be (Hall 1996).

As perhaps with same/different concept learning, discussed in next section, attempts to demonstrate Sidman equivalence in animals may be an example of disproportionate attention being devoted to a phenomenon influentially claimed to exist only in humans but without much thoughtful comparative or functional analysis. Nevertheless, what makes Sidman equivalence potentially important comparatively is its assumed similarity to conceptual abilities expressed in human language. As Hall (1996) points out, to the extent that equivalence class formation or functional categorization results from simple associative learning mechanisms, it should be phylogenetically very widespread. The apparent failure of pigeons to show full equivalence in Sidman's sense despite extensive testing implies that it requires something more.

6.5.4 Abstract or relational categories

Humans can classify things according to properties that emerge out of relationships among things. Do any animals use abstract categories (Herrnstein 1990)? One of the candidates most discussed in a comparative context is the same/different or matching concept (see Mackintosh 2000; Cook and Wasserman 2006). For instance, do animals trained to match to sample have a generalized ability to match? Pigeons trained with just a few stimuli (e.g., red and green) do not match novel samples (e.g., yellow and blue) but apparently memorize conditional rules ("If the sample was red, choose red; if green, choose green"). In contrast, various corvids such as rooks acquire a matching concept, transferring to novel colors, after similar treatment (Wilson, Mackintosh, and Boakes 1985; Mackintosh 1988). Monkeys and chimpanzees, too, match novel stimuli after exposure to just one matching problem, though the monkeys' transfer is not complete (D'Amato, Salmon, and Colombo 1985; Oden, Thompson, and Premack 1988). Pigeons do eventually acquire generalized matching if they are trained for thousands of trials with a large set of stimuli (review in Katz, Wright, and Bodily 2007).

However, matching to sample, in which the animal responds first to the sample and then chooses between the sample and a comparison, is a test of relative familiarity rather than identity, "Which did I just respond to?" rather than "Are these two things the same?" (Macphail, et al. 1995; Mackintosh 2000). Genuine same-different discrimination means classifying displays categorically as to whether items in it are all the same or not. This kind of discrimination, particularly whether pigeons can learn it, has arguably received undue attention (see Mackintosh 2000), partly because Premack (1983) claimed that only language-trained chimpanzees are capable of it. That is, given AX as a novel sample they choose BY over BB. However, chimpanzees with other kinds of experience also match "same" and "different" displays spontaneously (R. K. R. Thompson, Oden, and Boysen 1997; review in Zentall et al. 2008). Moreover, young chimpanzees implicitly categorize pairs of objects as the same or different without any special training (see

R. Thompson 1995). Given a pair of identical objects to handle, they are then more interested in a pair of nonidentical objects than in a pair of new objects that are identical to each other. Such behavior is also seen in young children but not in monkeys (Zentall et al. 2008).

A similarly low-level perceptual process or implicit knowledge is apparently responsible for pigeons' as well as monkeys' ability to categorize stimuli like those in Figure 6.19 as same or different (Cook and Wasserman 2006; Zentall et al. 2008). Pigeons were exposed to category discrimination training with pecks to one side key reinforced in the presence of a display of 16 identical elements; pecks to a second side key were reinforced in the presence of a display of 16 elements each different from the others. After being trained to 83% correct with 16 arrays of each kind, pigeons averaged 71% correct on arrays composed of novel symbols (Wasserman, Hugart, and Kirkpatrick-Steger 1995). Further analysis indicates that both pigeons and monkeys discriminate among such arrays on the basis of their variability, a feature measured continuously as entropy (see Cook and Wasserman 2006; Zentall et al. 2008; Wasserman and Young 2009). The more

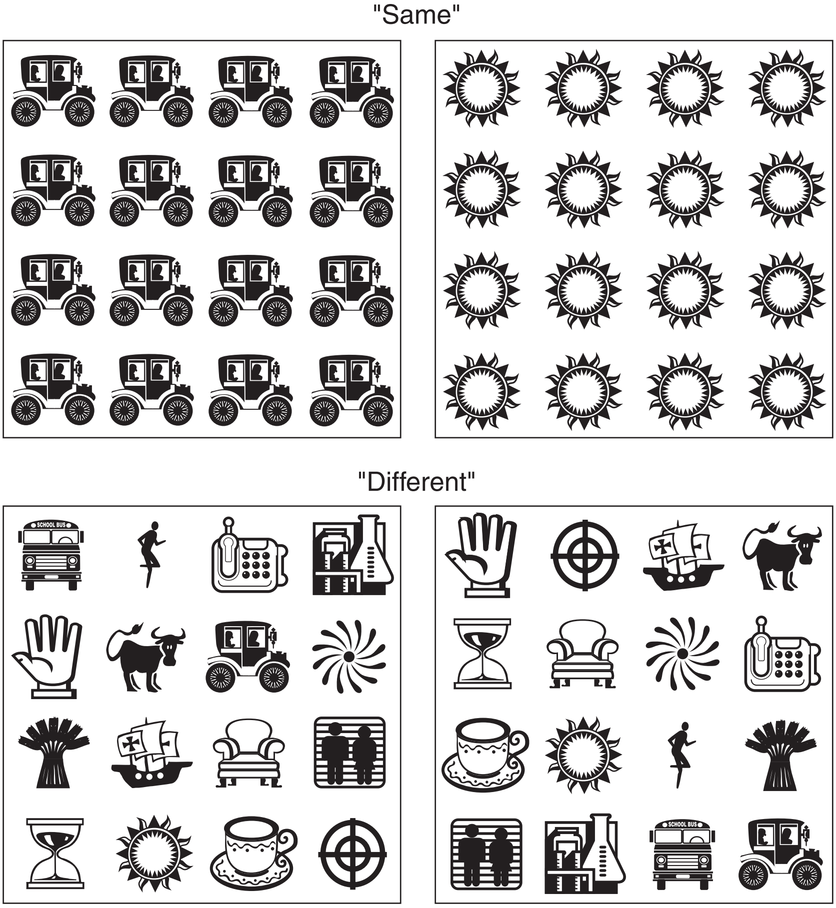


Figure 6.19. Examples of stimuli used to train pigeons in same/different discriminations. After Wasserman, Hugart, and Kirkpatrick-Steger (1995) with permission.

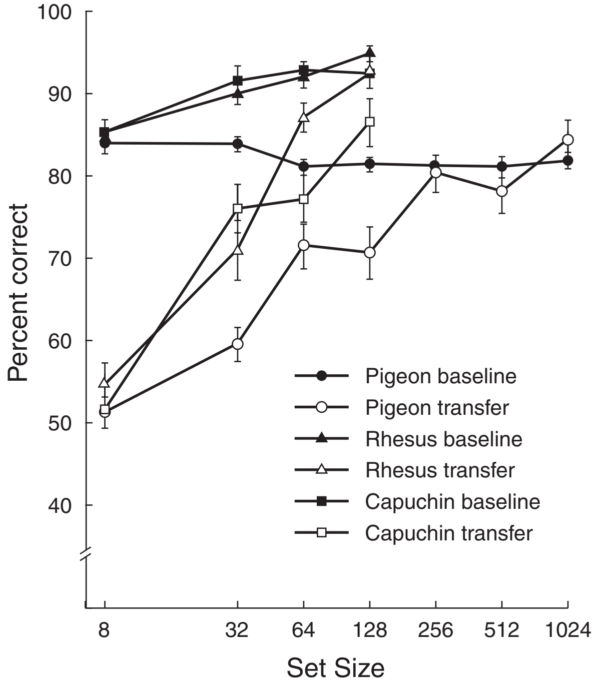


Figure 6.20. Progress of same/different classification learning with two items per display for pigeons, rhesus macaques, and capuchin monkeys as size of the set of possible items increased. The same stimuli and procedures were used for all species. All eventually classify novel stimuli as accurately as familiar ones ("transfer" data). Redrawn from Katz and Wright (2006) with permission.

different items in the display, that is, the more variable, the more likely it will be classified as different. But the human concept of *same* versus *different* is categorical: either things are the same or they are not, and in a task like the one for the pigeons, most—but not all—people behave accordingly (Castro, Young, and Wasserman 2006). Monkeys, however, are more likely to respond "different" the more different items there are (Smith et al. 2008). Reliance on variability in the displays probably accounts for why pigeons do poorly when the displays are reduced to two elements each, but they do eventually learn, albeit slower than monkeys (Figure 6.20). Importantly, all species represented in Figure 6.20 come to transfer perfectly to new displays, implying that they learn to rely on a feature that is independent of specific stimuli (Katz and Wright 2006; Katz, Wright, and Bodily 2007).

Consideration of this line of research suggests that the line between abstract concepts and direct perception of relationships is not easy to draw. Implicit knowledge of some abstract relationship may be embedded in a highly specific perceptual module without the animal being able to access it to control explicit, arbitrary, discriminative responses. Biological motion (R. K. R. Thompson 1995) and connectedness (Hauser 1996) might be other examples that are perceived directly. This same issue arises in discussions of whether animals have other kinds of conceptual knowledge about the physical and social worlds. They may behave as if having it but without showing the full suite of behaviors associated with explicit knowledge of, for example, the properties of objects or of others' minds (for further discussion see Hauser 2003; Vonk and Povinelli 2006). The capacities other species share with humans may be the building blocks of the fully elaborated, domain-general, consciously and verbally accessible, human capacities. Consistent with this interpretation, the continuous same/different discrimination process seen in pigeons and monkeys is still evident in humans doing the same task: even while correctly classifying arrays of items categorically, they are slower to respond "different" when the display has only a few different kinds of items than when each is different from the others see (see Wasserman and Young 2009). Nevertheless, the results of attempts to train nonhuman species on explicit use of a general concept *same* versus *different* are consistent with Penn, Holyoak, and Povinelli's (2008) claim that higher-level relational concepts are unique to humans.

6.5.5 Category learning, concepts, and natural behavior

The methods of category learning experiments can be used to discover whether and how animals categorize ecologically relevant stimuli. For example, cryptic palatable caterpillars tend to be neat eaters, leaving the leaves they have bitten with smooth contours like the contours of undamaged leaves, but unpalatable species are more likely to be messy eaters, turning leaves into ragged tatters. Captive black-capped chickadees can learn to search for insects on trees with damaged leaves (Heinrich and Collins 1983). Palatable caterpillars have enhanced their crypticity by evolving neat feeding behavior under pressure from the learning abilities of bird predators, an influence of learning on evolution to add to those mentioned in Box 6.3. P. Real et al. (1984) trained bluejays to respond differently to a slide silhouette of a cherry leaf damaged by a "neat" caterpillar than to one damaged by a "messy" caterpillar (Figure 6.21). After training on one exemplar of each type, the birds generalized to new exemplars. Furthermore, the responding associated with the "neat" leaves generalized to silhouettes of undamaged leaves. The shapes of these leaf silhouettes seem to be very salient, at least for bluejays (Cerella 1979).

Category learning procedures like those illustrated in Section 6.3 have been used extensively to understand how birds classify vocalizations (e.g., Sturdy et al. 1999; Braaten 2000). For instance, Bloomfield et al. (2003) tested whether black capped chickadees (*Poecile atricapilla*) classify the very similar calls of their species and the closely related Carolina chickadee (*P. carolinensis*) by species by training the birds on a category discrimination in which one of the sets of calls to be discriminated had calls from both species while the other had calls from only one. For example, all positive stimuli might be black capped chickadee calls but some negative stimuli came from each species. If the birds were sensitive to the between-species difference, they should more quickly learn the correct response for the different-species negative calls, which they did.

Not only perceptual but functional and relational categorization skills could be useful in the wild. As suggested in Example 2 at the beginning of the chapter, categorizing other group members by social relationship may be particularly important. An often-cited study by Dasser (1988a, 1988b) used a standard category

Figure 6.21. Stimuli used by Real et al. (1984). The leftmost "neat" and and "messy" leaves were used in training; other stimuli in those rows are examples of leaf patterns used in generalization testing. The bottom row shows probes representing undamaged leaves. Redrawn from Real et al. (1984) with permission.

Box 6.3 Evolution and Discrimination Learning: Models and Mimics

Brightly colored or patterned, noisy, or otherwise conspicuous prey tend to be bad-tasting or illness-producing, suggesting that their conspicuous features are warning predators to leave them alone. Although warning (*aposematic)* colors or other signals may be avoided when novel, potential predators usually must learn to avoid them. Many aposematic species have palatable *mimics,* palatable species that acquire protection from their resemblance to the unprofitable *model* species. For instance, some flies look like bees (Figure B6.3), some harmless snakes look like poisonous coral snakes, orange and black Viceroy butterflies have wing patterns remarkably close to those of poisonous Monarch butterflies. These are examples of *Batesian mimicry;* cases in which two or more unpalatable species resemble one another have traditionally been referred to as *Mullerian mimicry*.

The influence of predators' perception, learning, and memory on the evolution of mimicry and on relationships among populations of models and mimics has been widely discussed and investigated (for a comprehensive review see Ruxton Sherratt, and Speed 2004; Darst 2006). Consideration of basic learning principles generates a number of straightforward predictions about relationships between models and mimics. For instance, because stronger punishment should lead to faster

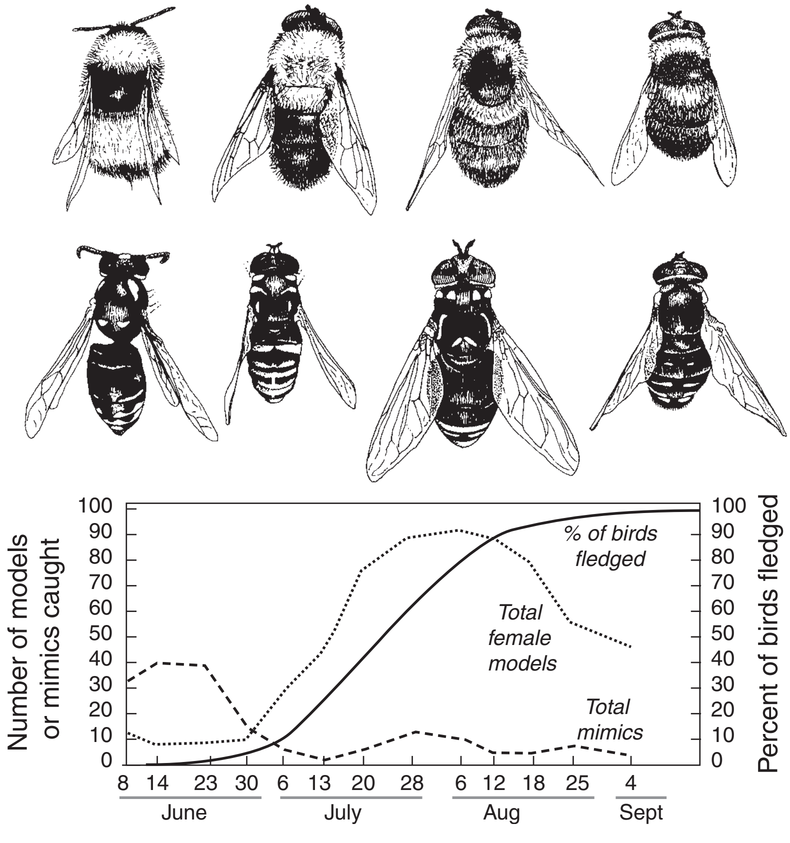


Figure B6.3. Top. Examples of Batesian mimicry complexes in which species of syrphid flies have evolved the appearance of stinging wasps and bees (Hymenoptera). In each row the insect on the left is the model bee or wasp; all the rest are different fly species (mimics). After a photograph in Waldbauer (1988) with permission. Bottom: Seasonal asychrony of stinging hymenoptera and their mimics in northern Michigan and the relationship of model and mimic abundance to the presence of naive predators, fledgling insectivorous birds. Redrawn from Waldbauer and LaBerge (1985) with permission.

learning and greater resistance to extinction, more aversive models should confer protection on larger numbers of mimics (Skelhorn and Rowe 2006). Because a stronger aversion should generalize more widely, more aversive or more numerous models should support cruder mimicry, and when two unpalatable species are present (i.e. in Mullerian mimicry), palatable (Batesian) mimics will be protected by the sum of generalization from both (Darst and Cummings 2006). Such predictions have been tested in numerous laboratory experiments with birds, often domestic chicks eating colored food flavored with quinine. However, careful analysis of natural predator-prey systems can also produce impressive support for them. For example, if predators can remember for a reasonably long time, a bird that has learned to avoid one species of insect in the fall may avoid a species that resembles it the next spring. The life histories of some mimics fit well with this scenario: they appear in the spring when they are avoided by experienced birds, but disappear by the time young, inexperienced birds have begun to forage on their own, which is when models appear (Figure B6.3; Waldbauer 1988).

Cryptic prey may benefit from being dispersed because this reduces the likelihood that predators will develop a search image for them (Chapter 3). In contrast, aposematic species should perhaps be aggregated. A group presents a stronger signal than does a single individual, and this would improve initial learning and later recognition by predators. Considering how warning coloration could evolve leads to the same prediction because a conspicuous bad-tasting individual will, by definition, probably be noticed by a naive predator and killed. Therefore it cannot pass on its characteristics to its offspring, but if the victim's relatives are nearby the predator may retain a memory of its bad experience long enough to give them a selective advantage. Thus warning coloration may evolve through kin selection. Laboratory experiments testing whether or why noxious prey are actually better avoided when aggregated (see Ruxton Sherratt, and Speed 2004) illustrate the intimate relationship between evolutionary and psychological issues in this area.

As Chapter 3 suggests, conspicuousness, distastefulness, and resemblance are all relative to the perceptual systems of the predators involved. Different kinds of warning signals confer protection against different kinds of predators. For example, many species of tiger moths are distasteful to both birds and bats. The species occurring in Southern Ontario vary in both visual conspicuousness and whether they produce ultrasonic clicks when stimulated by the calls of foraging bats. The former species tend to be diurnal and to be most abundant early in the season, when foraging by breeding migratory birds is at its peak. The latter, clicking, species tend to be nocturnal and to appear later in the season, when bats are doing most of their foraging. Thus contrary to suggestions that clicking and visual conspicuousness combine in an extraeffective multimodal warning signal for birds (which anyway would hardly hear the clicks), here different warning signals have evolved under pressure from different predators (Ratcliffe and Nydam 2008).

discrimination procedure to ask whether Java monkeys (*Macaca fascicularis*) could discriminate pairs of other monkeys on the basis of whether they were mother and offspring. One of the two subjects was trained in a discrimination task in which positive slides showed a mother-daughter pair from the subject's social group and negative slides showed a pair of unrelated monkeys. After training with five slides of a single mother-offspring pair and five different unrelated pairs, the subject monkey responded correctly to 14 out of 14 sets of slides showing new pairs of monkeys. Another monkey performed comparably on a matching to sample procedure. It is not clear whether perceptual similarity between mothers and offspring played any role here as it may in chimpanzees (Vokey et al. 2004) or whether performance reflected only knowledge of relationships gained in the subjects' social group, a kind of functional category. This could be tested by comparing performance with familiar versus unfamiliar mother-offspring pairs.

Animals that live in complex social groups may need to classify others simultaneously by dominance relationship and family (kinship group) as well as in other ways discussed in Chapter 12. Example 2 at the beginning of the chapter depicts a study designed to capture such multifeatured classification (Bergman et al. 2003) . Groups of related baboon females (*matrilines*) share a relative dominance ranking within their troop, but there are also dominance ranks within each matriline. This means that, from the point of view of a baboon listener, a submissive scream from a given female is to be expected if that individual was just threatened by a higher ranking member of her own matriline, but not if she was threatened by a lower ranking member of that matriline, because the latter sequence would represent a reversal in rank. Such rank reversals within families, however, are mere family squabbles, of less moment to an eavesdropper from another family than are reversals of rank between families, as these can presage social upheavals affecting the whole troop. Accordingly, a baboon hearing a submissive scream from one individual in response to a threat by an individual in a lower-ranking matriline should really take notice, as measured by how long she looks toward the source of the sound (a recorded simulation from a hidden loudspeaker in this experiment). Durations of looking were as predicted if baboons classify their social companions hierarchically, by family (rank reversals of which elicited relatively long looks) and by rank within family (reversals of which elicited shorter looks, slightly but not significantly longer than those elicited by control threat-scream sequences simulating a genuine dominance relationship). A critique of this study (Penn, Holyoak, and Povinelli 2008) suggests that the rank distance in within- versus between-family dyads for these mock interactions were a critical determinant of the results, but these were controlled appropriately (Cheney, personal communication, October, 2008). Japanese macaques recruiting allies for aggressive interactions seem to recognize the same sort of hierarchical classification (Schino, Tiddi, and Di Sorrentino 2006). They solicit help from higher ranking individuals, but only if they are not within the same family as their opponent.

Schusterman and colleagues (cf. Schusterman, Kastak, and Kastak 2003) have argued that classifying different members of the same family together is like learning an equivalence set. However, equivalence sets do not seem to capture the way in which individuals are simultaneously classified into, for example, both different families and social relationships within those families such as mother-infant, and dominant-subordinate. Rather, as Seyfarth and Cheney (2003a) have argued, this sort of multifaceted classification is more like the spontaneous chunking shown by rats and monkeys when required to remember many items of information (Chapter 7). For example, when rats have to remember the locations of 12 food items consisting of four pieces each of three food types, they behave as if organizing the information into categories corresponding to the food types. Seyfarth and Cheney's (2003a) analysis of the learning reflected by natural social classification is an outstanding example of how data on basic cognitive mechanisms from laboratory research can be integrated with information about natural behavior. Given the growing interest in comparative social cognition documented in Chapter 12, there are many possibilities for further development of such an integrative approach.

A relationship like mother-offspring or social dominance is abstracted from and in turn predicts many different behaviors of specific individuals. For example, a young monkey suckles from its mother, runs to its mother when frightened, is groomed and defended by its mother, and so on. In effect, different behavioral interactions belong together as signs of a particular relationship, and once that relationship is encoded as such on the basis of a limited number of observations, novel behavioral interactions can be predicted. Bovet and Washburn (2003) tackled the question whether captive rhesus monkeys perform this kind of classification by showing three monkeys short videos of other, unfamiliar, monkeys in a dominance interaction such as fighting, chasing, or giving a bared-teeth display. A film was stopped at the last frame and the monkey was reinforced for moving a joystick to make a cursor touch the image of the dominant monkey of the pair. Novel films continually introduced into the training set served on their first presentation as tests of generalization to new monkey pairs. When the monkeys were reliably able to indicate the dominant individual in one kind of interaction, for example, chasing, training moved on to another interaction, for example, the subordinate monkey moves away as the dominant approaches. Two of the monkeys showed some transfer across sets of films, as if using a concept of dominance. Transfer was far from complete, perhaps because the subjects actually had rather little social experience themselves and the images were small. However, this experiment suggests a tremendously effective way to probe the nature of animals' natural social knowledge.

6.6 Summary and conclusions

Any animal must respond differently to different things in its world, food and nonfood, mate and enemy. This chapter started by discussing discriminative behavior that is not obviously trained, as studied in classical ethology. Behavior toward complex natural objects generally turns out to be controlled by one or a few simple features, the ethologists' sign stimuli. The effective features have additive effects (heterogenous summation) and this may mean that objects never found in nature are more effective than natural objects (supernormality). Animals may discriminate among signals of their own species more accurately than among similar signals of other species, reflecting perceptual specializations and/or experience.

The discussion of how discriminations are learned among arbitrary stimuli in the laboratory in sections 6.4 and 6.5 parallels that of how natural discriminations are controlled, starting with classic studies of simple discrimination training and concluding with discrimination among categories of complex stimuli. It reveals similar principles as well, particularly when it comes to stimulus generalization and peak shift (which resembles supernormality) and in the additive effects of separable stimuli. The Rescorla-Wagner model (Chapter 4) provides a good account of how features that best predict reward or nonreward gain most control over discriminative behavior. Discrimination training also may have effects that cannot readily be explained as changes in excitatory or inhibitory strength. These include the acquisition of learning sets and possible changes in attention during successive reversal training.

Although discrimination among complex polymorphous categories like natural scenes and objects depicted in photographs was originally labeled "concept learning," no such special process seems to be required. To some extent the mechanism for learning to classify stimuli is flexible. Under some conditions some animals, such as pigeons, may simply memorize every item and its associated response, but category discriminations may also be solved by learning the features that distinguish the categories or by learning the central tendency or prototype of the category. Learning of functional categories (equivalence classes) approaches a little closer to what is thought of as concept learning, in that a common history of reinforcement binds perceptually disparate items together and mediates generalization among them. What nonhuman animals have so far not proven to learn is a truly abstract relational concept, one that transcends first-order or perceptual features of stimuli. This may be a kind of categorization that humans do not share with other species.

Equivalence class learning seems to play a role in social cognition and communication in nature, although other processes may also be involved. It would be surprising if equivalence classes, as well as the other kinds of categories that animals can learn in the laboratory, do not have counterparts in natural behavior. It is interesting to speculate on whether particular ways of classifying stimuli might be selected for in particular situations. For example, Nelson and Marler (1990) suggest that for songbirds, classifying songs on the basis of a species-specific prototype may be less useful than classification based on similarity to memorized exemplars because the latter can be fine tuned to the local sound environment.

This chapter contains some lessons that will be important to bear in mind later, when we get to comparative research on some abstract concepts that animals might have, including number and serial order (Chapter 10). We also look at tests of social and physical concepts, such as theory of mind (Chapter 12) and physical understanding (Chapter 11). The acid test of a concept is always generalization to novel stimuli that share only the abstract or conceptual relationship under test with the training stimuli. Defining stimuli for such tests is not necessarily easy. Just as with the pigeons trained to discriminate trees from nontrees, it is critical to bear in mind that effective behavior can be based on cues and kinds of representations very unlike those that people would use to solve the same task and try to imagine what they might be.

Further reading

Tinbergen's (1951) *The Study of Instinct* is highly recommended as an introduction to ethology. Dooling et al. (1990) provide a good introduction to the use of multidimensional scaling to study natural perceptual categories, as does the chapter by Nelson and Marler (1990). Fetterman (1996) thoughtfully discusses the issue of "what is a stimulus," especially as it applies to psychological research on category learning. For reviews of recent work on the psychology of discrimination learning and classification in animals, excellent sources are the online "cyberbook" *Avian Visual Cognition* (R. Cook 2001a) and the book edited by Wasserman and Zentall (2006), particularly Chapters 16–21. In the former collection, the contribution by D. S. Blough (2001) is especially recommended. Zentall et al. (2008) is a useful short review of recent work on categorization, but for an in-depth review of the research started with the same/different paradigm in Figure 6.19 see Wasserman and Young (2009). Mackintosh (2000) is an excellent overview from an associationist viewpoint. Ghirlanda and Enquist (2003) as well as Cheng (2002) discuss phenomena and theories of generalization from both psychological and behavioral ecological perspectives. *Avoiding Attack* (Ruxton, Sherratt, and Speed 2004) contains a clear and well-illustrated discussion of the various forms of mimicry along with other aspects of the arms race between predators and prey.

7
Memory

Forming a search image, acquiring a conditioned response, recognizing one's mother: all are examples of learning. But they are also examples of memory because new information is being retained from one occasion to the next. Nevertheless, in psychology *learning* and *memory* define separate bodies of research. Research on learning has traditionally dealt with how information about relationships between events is acquired, as measured by fairly long-lasting changes in behavior. Research on memory, in contrast, deals with how information is stored, retained and retrieved. The cognitive changes of interest often take place rapidly, may not be very long lasting, and may be read out in a variety of behaviors. But parts of this description apply to examples of "learning." For instance, flavor aversions can form in one trial, and Pavlovian conditioning may influence a whole behavior system (Chapter 4). Thus there is good reason to question the traditional dichotomy between *learning* and *memory*. It is simply disregarded in contemporary research on the neuroscience of memory in which studies of changes in the brain during learning are labeled as studies of memory (Section 7.5.3).

From early in the twentieth century until the 1960s, most research on memory was done with human subjects even though much of the theorizing that drove it came from associative models based on research with other species. The "cognitive revolution" of the 1960s turned the tables. Research on human memory began to focus on the nature of information processing and representation. Research on animals followed (Chapter 1). Early research on animal memory was often quite anthropocentric, designed to discover whether representatives of convenient species like Norway rats or pigeons behaved like people when they were tested in a parallel way. Some of this research took on a life of its own, directed more at the nature of particular species' performance in particular paradigms than at the nature of memory generally. In the early twenty-first century, studies of human and of nonhuman memory are increasingly reconnected in research on the neurobiological and genetic mechanisms of memory (Dudai 2004; Pickens and Holland 2004; Roediger, Dudai, and Fitzpatrick 2007; Eichenbaum 2008), and in the research on metacognition and episodic-like memory discussed at the end of this chapter, among other ways.

We start by looking at whether the properties of memory can be predicted by considering what memory is used for and sketching a framework for asking questions about memory. Studying memory in animals poses the same problems as studying perception: whereas adult humans can be asked "What do you perceive?" or "What do you remember?," subjects of other species have to be asked in other ways, some of which are described in Section 7.2. Section 7.3 summarizes the main conditions that affect memory. Section 7.4 reviews several research programs testing the notion that species differ in how much or how long they can remember. Theories about the contents and mechanisms of memory are discussed in Section 7.5. Recent years have seen clever experiments designed to test for memory processes that, in humans, are accompanied by distinctive states of awareness. The challenges posed by this research, on metacognition and episodic-like memory, and the important general principles it illustrates are discussed in Section 7.6.

7.1 Functions and properties of memory

7.1.1 What are memory and forgetting for?

What determines which information is stored, how it is expressed in behavior, and how long it is retained? These questions map into functional questions: what information is useful, what is it useful for, and how long is it useful? The first two of these were addressed in Section 4.3, on the function and evolution of learning. With respect to memory, the principal functional question is how quickly memories should be acquired and how long they should be retained, or, on the flip side, how quickly forgotten.

As William James (1890, vol. 1, 679) wrote, "forgetting is as important a function as remembering." Not forgetting may have a cost in inappropriate behavior when conditions change. Keeping memories perfectly accurate for long periods may also have a cost in neural circuits and genetic machinery for their maintenance and repair (Dukas 1999). Given that forgetting is therefore to be expected (see also Kraemer and Golding 1997), the rate of forgetting should evolve to track the rate at which the environment changes: the more quickly old information becomes useless, the more quickly it should be forgotten. In other words the probability of retrieving a particular memory should track the probability that it is needed (Anderson and Schooler 1991). Two variables predicting the likelihood that information will be needed now are how often it was needed in the past and how long ago it was last needed. These correspond to *practice* and *retention interval,* respectively, in tests of memory. To discover whether the effects of practice and retention interval do match the properties of the environment, Anderson and Schooler (1991) looked at three sources of data on the temporal distribution of information in the world. One was words in the headlines of the *New York Times*. These reflect demands on memory use because when a word like *Iraq* or *Beatles* appears, the reader has to retrieve a memory of its significance in order to interpret the headline. A given word was less likely to appear the longer since it last appeared and the less often it had appeared in the past (Figure 7.1). Data from experiments on memory retrieval as a function of time and number of past exposures in humans and other species resemble these functions (Figure 7.1; Wixted and Ebbesen 1991). Because Anderson and Schooler's is a proposal for why forgetting has evolved as it has, changing the probability that information is needed within an animal's lifetime (e.g., Sargisson and White 2004) should not necessarily affect memory duration.

With some success, Anderson and his colleagues (Anderson and Milson 1989; Anderson and Schooler 2000) have explored ways in which the properties of memory in humans can be related to the properties of information-retrieval systems (see also

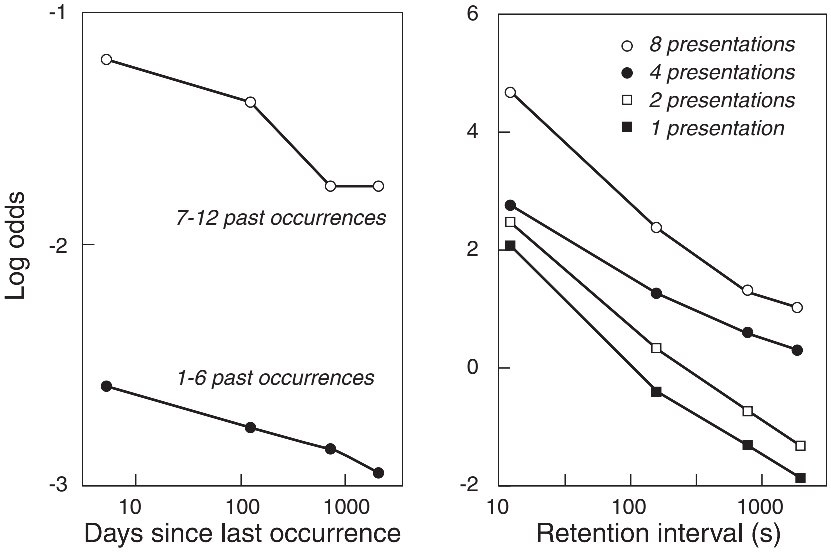


Figure 7.1. Left panel: The odds of a word appearing in the headline of the *New York Times* related to the days since it last occurred and the number of times it occurred in the past. (*Odds* is defined as follows: if p is the probability of an event, $q = p/(1 - p)$ is the odds of that event.) The right panel shows forgetting curves from a study of human memory that have an analogous pattern. Figure 7.5 shows analogous data for pigeons. Redrawn from Anderson and Schooler (1991) with permission.

Nairne, Pandeirada, and Thompson 2008). But our ancestors were not reading *The New York Times,* so to consider Anderson and Schooler's (1991) results relevant to the evolution of memory, one has to assume that headlines in a late twentieth-century Western newspaper reflect a general property of events in the world. There have been few comparable attempts to test how well the properties of memory in other species match the properties of their environment. As one example, foraging theorists have discussed what memory window should be used for estimating fluctuating quality of food patches (see Chapter 11 and Box 7.1). Averaging over too long a time may not allow effective tracking of patch quality, but with too short a memory window behavior will be unduly influenced by local fluctuations.

Box 7.1 Forgetting and Temporal Weighting

When a resource frequently changes in value, if it has not been sampled for a while an animal should respond as if the resource has the average of its past values. For instance, if 2/3 of the time Patch A has food while B has none, and 1/3 of the time the reverse is true, and the forager has not sampled either patch recently, its best bet is to visit A regardless of which patch was better on its last visit. Under some conditions, this *Temporal Weighting Rule* (Devenport et al. 1997) predicts behavior indistinguishable from the result of forgetting, but in situations for which its predictions differ, behavior fits those predictions.

One illustration is a field study of ground squirrels and chipmunks (Devenport and Devenport 1994). Two platforms that could be loaded with sunflower seeds were set up in an area that golden-mantled ground squirrels (*Spermophilus lateralis)* and least chipmunks (*Tamias minimus*) had been trained to visit. One platform, A, was always baited until the animals reliably chose it first. Then the second platform, B, was immediately baited instead until animals were visiting it first. Choice of A vs. B was tested either 1 hour or 24 hours later. Animals tested immediately always chose B first, but animals tested 24 hours later chose B only about 50% of the time. This finding that could of course reflect either forgetting or temporal weighting. It could also be interpreted as spontaneous recovery (see Chapter 4) of the tendency to visit A which had been extinguished when baiting of B began. The same is not true of the results of a further experiment with three platforms—A, B, and C. A was baited twice as often as B, and C was never baited. Here the temporal weighting rule predicts that B will be chosen immediately after a trial in which it was baited, but A will be chosen after a delay. This pattern of choice has been found not only in this study with chipmunks and ground squirrels (Figure B7.1), but also in laboratory studies with pigeons (Mazur 1996) and rats (Devenport et al. 1997; Devenport 1998).

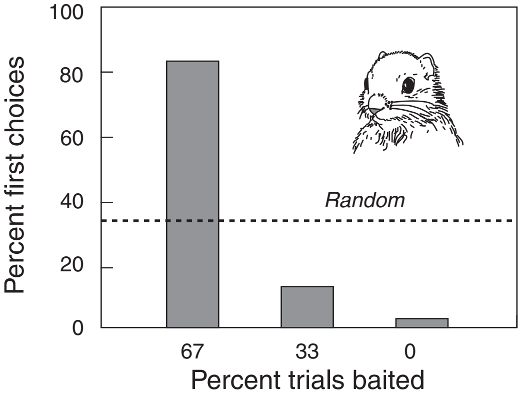


Figure B7.1. Percent of trials on which free ranging ground squirrels chose each of three feeders first 24 hours after the last trial as a function of the overall percent of previous trials on which each one had been baited. Data from L. D. Devenport and J. Devenport (1994).

The procedure in these experiments is essentially successive reversal learning. The discussion of successive reversals in Chapter 6 suggested that interference in memory is responsible for the fact that extended reversal training results in random choice of two equally rewarded alternatives at the beginning of each new session. Spontaneous recovery of the response not most recently reinforced may also play a role (Mazur 1996; Rescorla 1996; Devenport et al. 1997; Devenport 1998). Currently, the temporal weighting rule itself is one current candidate for an account of spontaneous recovery (Rescorla 2004). In any case, along with the study of Cheng and Wignall (2006) discussed in the main text, research designed to test the temporal weighting rule shows how changes in behavior with time since training do not necessarily reflect loss of memory.

A functional approach suggests that some things should be remembered longer than others. In a seminal paper, Sherry and Schacter (1987) developed the notion that acquiring, storing, and using different kinds of information demands adaptively different memory systems (or cognitive modules). The existence of two kinds of spatial memories—path integration and landmark memory—in desert ants, *Cataglyphis fortis,* provides a nice test of this idea within a single species and behavior system. The path integration system records position on the current journey by keeping track of an animal's current distance and direction from home on the basis of internally generated cues, thereby enabling it to return straight there when it finds food or is frightened by a predator (Chapter 8). Because successive foraging trips may have different lengths and directions, the path integration system would not be expected to retain information for more than a few hours, longer than an ant could stay away from the safety of its nest. In contrast, the system for learning visual landmarks should integrate information about stable features of the environment over successive trips. As these functional ideas predict, ants trained without landmarks and then captured and held before being allowed to home could not home accurately after 2 to 4 days, whereas ants that had equivalent experience in the presence of landmarks showed no forgetting after 20 days (Ziegler and Wehner 1997). The ants' path integration system uses only information from the current trip (Cheng, Narendra, and Wehner 2006; Narendra, Cheng, and Wehner 2007). Averaging information over successive journeys of different lengths would not be useful as it could lead the ant somewhere between the currently required distance and the one before.

Sometimes animals should retain information they have not needed for many months or even years. For example, fur seal mothers and offspring recognize each others' vocalizations when they return to the breeding grounds after a year or more away (Insley 2000). Birds' memories for their neighbors' songs (Box 5.1) are retained from year to year and used if they return to the same territories after migration (P. McGregor and Avery 1986; Godard 1991; Stoddard. et al. 1992). This song memory is distinct from that used in learning song in the first place (Box 13.2). After five months in hibernation Belding's ground squirrels still discriminate odors of littermates from those of strangers, but they do not appear to recognize the odors of unrelated individuals that they had recognized before hibernation (see Section 5.4 and Mateo and Johnston 2000b). Mateo and Johnston suggest that unrelated individuals may not be so important to remember through hibernation. This is an intriguing example of possible adaptive differences in memory, but the apparent difference in forgetting could reflect the fact that kin recognition is a matter of matching other individuals' odors to one's own (see Chapter 5) and thus does not depend on memory. If dependent on memory, it could reflect greater prehibernation exposure to littermates than to unrelated individuals

Animals that return annually to the same breeding or feeding grounds as the fur seals do should retain information that is useful there rather than pay the cost of relearning. For this reason some migratory species might be expected to have especially good long-term memory, a prediction put to the test by Mettke-Hofmann and Gwinner (2003) in a comparison of migratory garden warblers (*Sylvia borin*) and closely related nonmigratory Sardinian warblers (*S. melanocephala momus*). All the birds were exposed to seasonal changes in day-night cycle while held in captivity in Germany. When the garden warblers would have been starting toward Africa, each bird was exposed to two large cages ("rooms") adjoining its home cage. One was furnished with artificial geranium plants and one with artificial ivy. Only one of the rooms had food. Separate groups of birds were tested for their memory of the better "habitat type" at six retention intervals ranging from four days to one year. At the three longest intervals (5.5 months or more), as predicted the migrants showed a significant preference for the vegetation type associated with food whereas the nonmigrants did not. The case for species differences in memory here would be stronger if all birds had been tested at end of the training phase to be sure they learned the task to the same degree initially. A similar approach has been used to test population differences in memory in sedentary and migratory populations of a single species (cf. Cristol. et al. 2003). Pravosudov, Kitaysky, and Omanska (2006) found a difference in both spatial memory and hippocampal volume in favor of migratory as opposed to nonmigratory white-crowned sparrows (*Zonotrichia leucophrys*), but they tested the birds only after a 20-minute retention interval. All these studies are subject to the usual problems with comparative studies of memory discussed later in the chapter and therefore are more suggestive than conclusive, but they illustrate the rich possibilities for future studies.

7.1.2 Properties of memory

The same three questions can be asked about memory as were asked about learning in Chapter 4. *(1)* What are the conditions under which information is retained? Answering this question involves describing those conditions (Section 7.3) and understanding why they have the effects they do (Section 7.5). *(2)* What are the contents of memory? This question, about the nature of representation in memory, can be answered at different levels of detail. For example, we might infer that the location of food is remembered by observing that a hungry animal goes back to where it last found food. But the content of that memory might be the position of the food relative to nearby landmarks, the path to the food, or something else. *(3)* What are the effects of memory on behavior? Traditionally, it was assumed that a memory can be accessed in a variety of ways. For example, a subject shown a list of words can later be asked to find them in a larger list or write them down or call them out. A rat can indicate which arms of a maze it remembers by selectively returning to those arms or by avoiding them. However, humans can access some memories only through certain kinds of behavior but not verbally, as discussed in Section 7.6. And just as with learning, memory is distinguished theoretically from performance, so it is important to keep in mind that the behavior taken as expressing memory can occur for other reasons (Bouton and Moody 2004; Thorpe, Jacova, and Wilkie 2004).

7.2 Methods for studying memory in animals

Figure 7.2 shows a standard conception of the structure of memory. Input is first processed in sensory registers and stored temporarily in a *short-term store* (or *short-term memory, STM*), where it is accessible to decision processes. The short-term store also includes information called up from the *long-term store* (or *long-term memory, LTM*). Current input and stored information about its significance together with motivation control response output. Some of the contents of the short-term store are quickly lost, while others become part of long-term memory. One focus of research

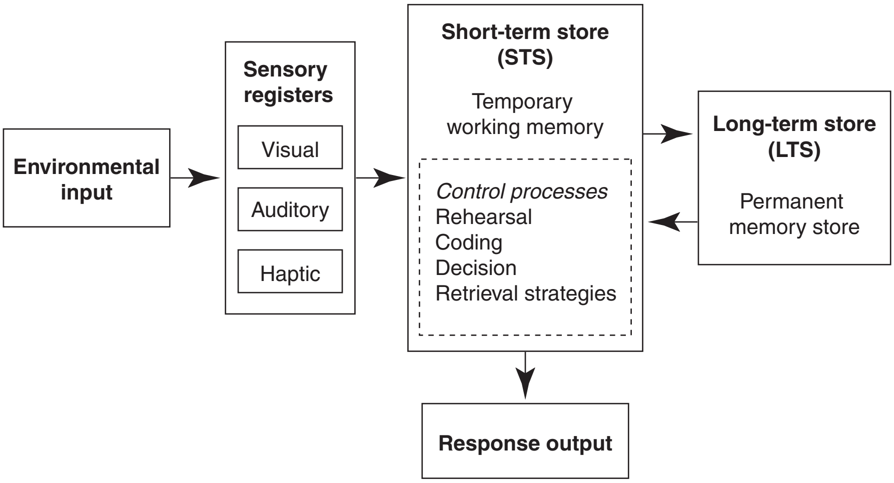


Figure 7.2. The hypothetical flow of information through memory. Redrawn from Baddeley (1995) with permission.

on human memory has been the nature of these memory stores and their relationship. The most closely parallel behavioral work with nonhuman species is that of Wagner and his associates using habituation, discussed in Chapter 5.

Those who work with animals sometimes distinguish between *working memory* and *reference memory.* Working memory here does not necessarily mean the same thing as working memory in humans (Baddeley 1995). Working memory in experiments with animals is defined operationally as memory for events on a specific trial, whereas reference memory is memory for the unchanging characteristics of a task (Honig 1978). For example, a test of memory might require the animal to learn "food comes out of that hole in the wall" or "you will get food if you choose the color you saw most recently." This information about what happens on every trial is part of reference memory. Information like "the most recent stimulus was a red square" is part of working memory. As we will see, the duration of working memory may depend on the task.

With humans, *recognition* or *recall* can be tested. That is, a person can be presented with a stimulus and asked "Have you experienced this before?" (recognition) or simply instructed to "Tell me what you remember" (recall). Recognition is typically better than recall of the same material, possibly because there are more *retrieval cues* in the test of recognition (Section 7.3.3). Most tests of animal memory are tests of recognition (but see C. Menzel 1999). Often the same items are used over and over, so the animal is really being trained in a *recency discrimination.* That is, rather than discriminating something familiar from something novel, it has to discriminate the stimulus presented most recently from other familiar stimuli presented earlier in the same session or in previous sessions (Wright 2006). Still, in tests of memory for lists of words, human subjects are essentially asked whether familiar words were presented in the experiment, not whether they have ever seen them before. Recognition memory is often distinguished from *associative memory,* memory for whether reward or nonreward accompanied an event in the past. When the same items are used repeatedly, recognition may be difficult to disentangle from effects of reinforcement history (Macphail, Good, and Honey 1995). Repeated presentations of the same items may also drive down performance and obscure effects that are apparent with items that appear no more than once per session, that is, *trial-unique* items (Wright 2006)

7.2.1 Habituation

The logic of habituation experiments is simple: if behavior toward an eliciting stimulus changes from one occasion to the next, and if motivational and sensory causes of the change can be ruled out, information about the earlier presentation must have been stored in memory. A strength of habituation as a test of memory is that it can be used with species and stimulus-response systems where training is difficult or perhaps impractical because large numbers of animals are to be tested, as in neurobiological studies. Its corresponding weakness is that it can be used as an assay of memory only for events that naturally evoke a well-defined response. As discussed in Chapter 5, much recent work has made use of the fact that animals may reveal what they have spontaneously encoded about events and objects by looking at them or exploring them when they change. For example, up to an hour after encountering an object in a particular location and context rats given a test like that depicted in Figure 7.3 show evidence of memory for the particular configuration of object, place, and context, a possible example of episodic memory (Section 7.6; Eacott and Norman 2004).

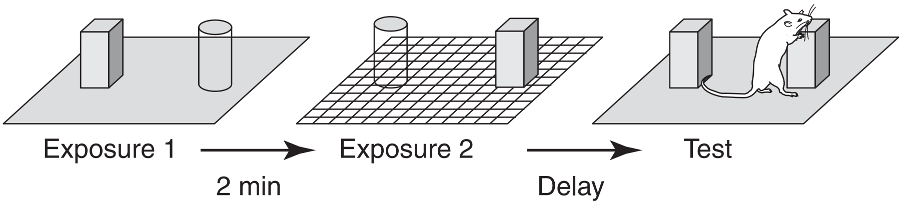


Figure 7.3. Procedure for testing encoding of place, context, and identity during habituation. In each distinct "exposure" context, the two objects are arranged differently. Some time ("delay") after rats have explored them in each context, they encounter two copies of one object in one of the exposure contexts. Preferential investigation of the object that is in a new location for that context is evidence for episodic-like memory. After Eacott and Norman (2004) with permission.

7.2.2 Delayed response tasks

Hunter (1913) was one of the first to use a delayed response test of memory for animals (Boakes 1984). He trained rats, raccoons, and dogs in appropriately sized versions of the apparatus shown in Figure 7.4 to approach the door under a light to obtain food. The light was over a different door on each trial so that the animal had to approach the light regardless of its location. Then the animal was restrained in the start area while the light was turned on briefly. If it could still choose the correct door when released after the light went out, it must have retained information about the location of the light during the delay, the *retention interval.* Hunter wanted to discover whether animals had "ideas,"

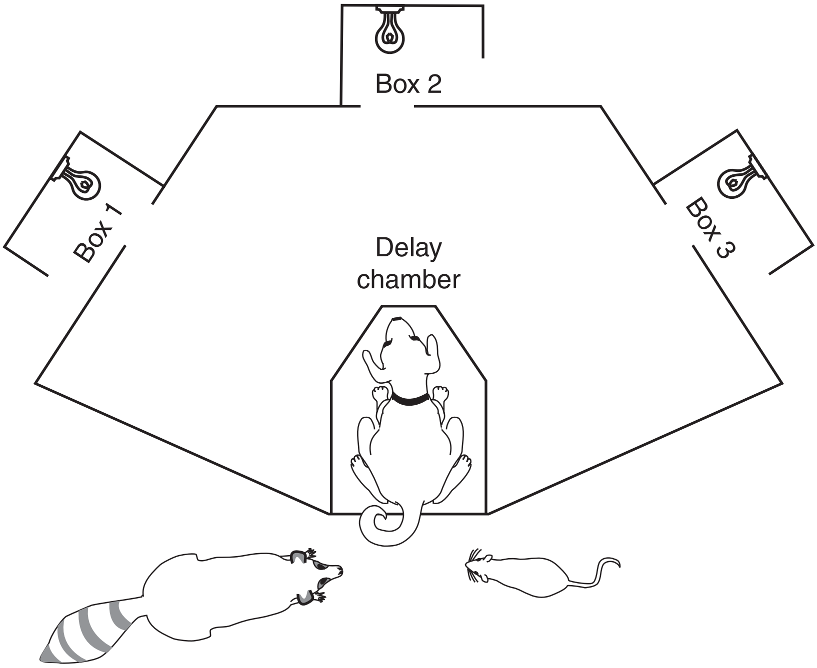


Figure 7.4. Schematic view of Hunter's apparatus for studying delayed response. The size was adjusted for the different species. After Maier and Schneirla (1935/1964) with permission.

representations of objects or events that were not present at the time of responding. But some animals performed well by facing the correct door during the delay. Disrupting this orientation by removing the animal from the start area during the delay could reduce choice to chance levels.

Figure 7.5 depicts a modern version of Hunter's task, the *delayed matching to sample* procedure, as it might be used for pigeons in an operant chamber. A trial begins with display of a *sample,* the to-be-remembered stimulus. The bird is generally required to peck the sample a number of times to turn it off and advance to the next stage of the trial. This ensures that the animal has actually seen the sample and gives the experimenter some control over the duration of exposure to it. Primary reinforcement such as food is usually not given for responding to the sample, so if the animal chooses a stimulus like it in the test phase this is despite earlier nonreward. The sample is separated from the test phase of the trial by a retention interval (*RI*). At the end of the RI the animal is presented with a choice between the stimulus it saw before,

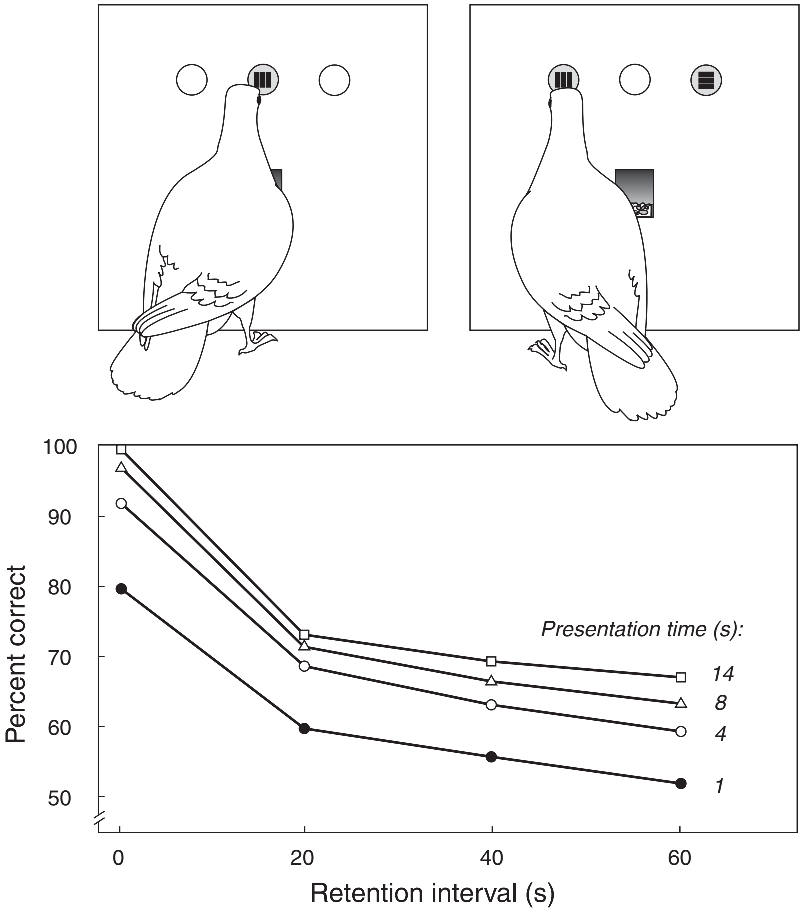


Figure 7.5. Typical delayed matching to sample procedure for pigeons. Here the pigeon is reinforced (by grain appearing in the opening below the keys) for pecking the pattern that matches the pattern pecked in the first part of the trial. Redrawn from Wright (1991) with permission. Lower panel: Effects of retention interval and duration of sample exposure on pigeons' matching to sample performance. Redrawn from Grant (1976) with permission.

say red on the key, and a *comparison stimulus,* say green. Because these stimuli are on two side keys whereas the sample was on the center key, memory for the sample's location cannot influence choice in the test. If the bird chooses correctly, it will be reinforced; if it chooses incorrectly it may proceed directly to the intertrial interval or it may be punished or corrected. For example, the lights in the testing chamber may go out for a few seconds, or the trial may be repeated until the bird makes the correct choice. In any case, an intertrial interval (*ITI*) ensues and then a new trial begins. The identity of the sample and the location of the choices on the side keys change randomly from trial to trial. A typical daily session might include 100 or more trials, and the same small set of stimuli (often just two) is used over and over. What the animal is exposed to, then, is a rapid-fire series of events: "Red." . . . "Was it red or green?" . . . "Green." . . . "Was it red or green?" . . . "Green." . . . "Was it red or green?" . . . Small wonder that pigeons' performance in this type of task is typically quite poor in absolute terms, even after thousands of trials of training. Figure 7.5 shows an example. Of course, the precise slope and height of forgetting curves depend on details of the testing procedure like those discussed in Section 7.3 (van Hest and Steckler 1996; White, Ruske, and Colombo 1996; Wright 2006).

Memory for a sample can also be tested by reinforcing choice of the comparison that differs from it, that is, *delayed nonmatching to sample* or *oddity*. Despite its name, pigeons generally do not acquire a concept amounting to "choose the comparison stimulus that matches (or doesn't match) the sample" in these procedures, although some animals do (Chapter 6). Indeed, pigeons do just as well at *symbolic matching* as at literal matching (for examples see Zentall et al. 1989). In symbolic matching, each sample is associated with one or more arbitrary comparisons. For example, choice of a horizontal line is reinforced following a red sample, whereas choice of vertical is reinforced following green. There are many other variants on the basic delayed matching test. In *delayed alternation,* an animal is reinforced for responding to the stimulus it didn't just respond to. For instance, a rat may be allowed to visit one arm of a T-maze, then replaced in the start box and required to visit the opposite arm. After doing so, it must visit the first arm again, and so on.

7.2.3 The radial maze

In typical delayed matching tasks, memory of a single sample is not retained for more than a few seconds or minutes. Imagine, then, the sensation created by an article entitled "Memory for places passed: Spatial memory in rats" (Olton and Samuelson 1976) reporting that rats could retain information about all the arms they had visited in an 8-arm *radial maze* for at least several minutes. As devised by Olton and Samuelson, a radial maze (Figure 7.6) consists of eight flat, unwalled arms, elevated (so rats don't climb off), each about a meter long, radiating out from a central platform. The maze is placed in a normal, lighted, laboratory room, with pieces of furniture, windows, doors, posters on the walls, in short, numerous objects to provide the rat with cues about where it is on the maze. At the start of a trial, a small piece of food is concealed at the end of each arm. The rat is placed on the central platform and allowed to remain on the maze until it has collected all the food. Once rats have been accustomed to the maze, they collect all the bait very quickly and seldom revisit already-emptied arms while doing so. Various control procedures have shown that they do not use odors either from the remaining food or from their own tracks

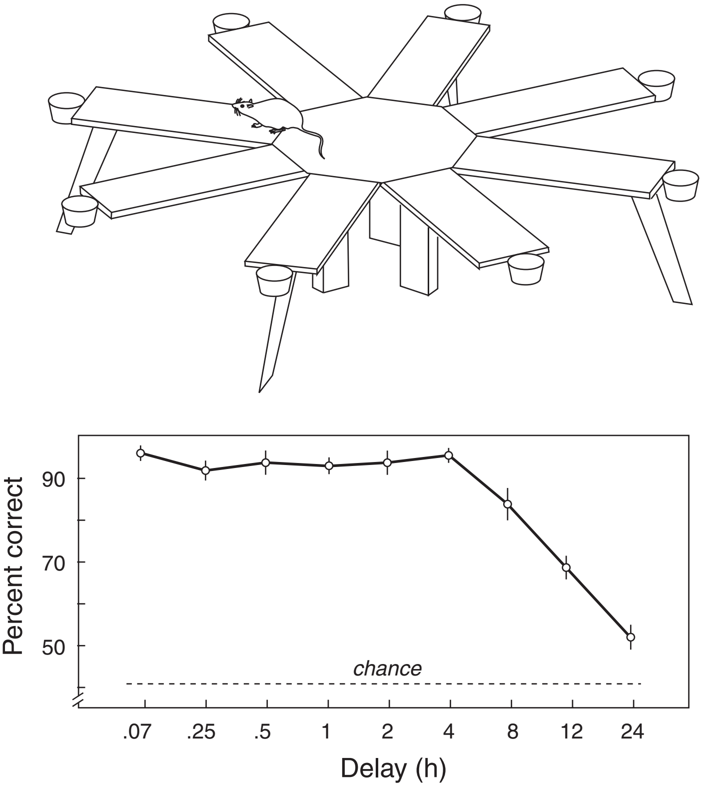


Figure 7.6. A rat on an eight-arm radial maze with a food cup at the end of each arm, redrawn from Roitblat (1987) with permission. Data are mean (+ SE) proportion correct choices out of the first four choices following a retention interval during which rats were removed from the maze, having already visited four arms. Redrawn from Beatty and Shavalia (1980) with permission.

down the arms. Individual rats generally do not repeat the same pattern of visits from one trial to the next, nor do they follow an obvious rule in choosing successive arms (Olton and Samuelson 1976; W. Roberts 1984). Thus, they are exhibiting working memory for the locations already visited on the current trial.

In most tests of human memory, the experimenter chooses the items to be remembered, but in the radial maze as just described the animal chooses them because it controls the order of arms it visits. The to-be-remembered items can be controlled in the radial maze, however, by placing doors around the center platform and opening only one or a few at a time. This simple modification also allows control over the interval over which the experimenter-selected "items" must be remembered. In a typical procedure that does this, a rat is placed on the maze with four doors open. Once the rat has collected food from these arms, a retention interval ensues, which the rat may spend off the maze. Then all eight doors are opened and only the arms not visited in the first phase of the trial are baited. With this procedure, rats perform better than chance at retention intervals up to 24 hours (Figure 7.6). Radial mazes and equivalent arrangements have become standard for testing working memory in all sorts of species, including hummingbirds collecting nectar from artificial flowers in the field (Healy and Hurly 1995, 2001).

7.2.4 Delayed matching, the radial maze and foraging

In Figure 7.5, one item is completely forgotten in a few seconds. In Figure 7.6, four items are retained for hours. Why do pigeons perform so much worse on operant delayed color matching than rats do on the radial maze? A number of reasons immediately suggest themselves: rats versus pigeons, "natural" versus "unnatural" tasks, spatial versus nonspatial tasks, rich multiple cues versus impoverished single cues. Less obviously, the typical testing regimes differ drastically. Rats are generally given just one trial of eight choices a day on a radial maze, whereas a daily session of operant delayed matching consists of many trials. No wonder the animal performing the operant task is sometimes more confused about which stimulus it saw last! The two tasks typically differ enormously in difficulty as *relative recency discriminations,* in terms of the potential for *interference* between one trial and the next (Section 7.3). Moreover, in delayed matching of colors the stimuli to be discriminated differ in only one respect, whereas the arms of a radial maze typically differ in many respects. The richness of cues also helps to make the spatial task easier. Operant delayed matching tasks incorporating both spatial and color cues give much better performance than those with more impoverished cues (Wilkie and Summers 1982; Zentall, Steirn, and Jackson-Smith 1990). Conversely, folding the arms of a radial maze together so they all point the same way degrades rats' perfomance (Staddon, 1983).

The variety of cues available and the fact that the animal travels from place to place rather than being passively exposed to the to-be-remembered items makes the radial maze resemble some natural foraging problems. Animals that consume nectar, such as bees and hummingbirds, feed from sites are not replenished immediately. Some apparently adopt a systematic pattern of visits rather than relying on working memory. For example, bumblebees (e.g., Hartling and Plowright 1979) collect nectar from closely spaced blossoms by following a fixed movement rule: "start at the bottom and always move to the next higher inflorescence," but they may also learn the locations of rewarding flowers (J. Burns and Thomson 2006). Some nectar feeding birds appear to follow an habitual "trapline" (Kamil 1978; Gill 1988; but see Healy and Hurly 2001). Because different kinds of flowers refill at different rates, nectar feeders might be expected to adjust their intervisit intervals on the basis of experience. Hermit hummingbirds seem to do this (Gill 1988). After being exposed for a few days to two "species" of artificial flowers, one of which refilled 10 minutes after being depleted and one after 20, rufous hummingbirds (*Selasphorus rufus*) learned to time their visits to each species appropriately (Henderson,. et al. 2006), a natural example of the interval timing discussed in Chapter 9.

Scatter hoarding animals retrieving their stores also face the problem of remembering where they have collected food and not going back. Sherry (1984) allowed black-capped chickadees to retrieve part of a batch of stored food one day and the rest the next day. On the second test, the birds visited storage sites still holding food rather than those they had already visited (see also Shettleworth and Krebs 1982). Reinforcement would seem to dictate that an animal should return to a place where it got food, not go somewhere else, so this behavior, like that of rats in radial mazes (Maki 1987) and hummingbirds collecting nectar, indicates that the animal is responding to food as information, not reinforcement. Shifting away from a recently rewarded site rather than revisiting it immediately (i.e., a *win-shift* rather than a *win-stay* strategy) might be an adaptation to foraging on food sources that can be depleted in one visit, but of course the forager should return to such a food source when it has had time to refill. Thus win-shifting might be replaced by the opposite propensity after a suitable time, and indeed one species of Australia honeyeater does show such an effect (Burke and Fulham 2003).

7.3 Conditions for memory

Not surprisingly, the conditions that influence memory are similar to those that influence association formation (Chapter 4) and recognition learning (Chapter 5). The more salient, long-lasting, or frequent an event, the better it is remembered. In the study of memory, attention has been directed not only at the conditions present at T1 (the time of input or *encoding*) but also at the conditions between T1 and T2, that is, during the retention interval, and at how the conditions at T2, the time of test, influence the *retrieval* of memories. The relationship of a target event to events in the past may also matter, as in the example of proactive interference in Figure 7.8. And as with learning, because the effect of experience may be expressed only under certain conditions or only in some behaviors, competence must be distinguished from performance (Bouton and Moody 2004; Thorpe., Jacova, and Wilkie 2004).

The primary index of memory is the influence of events at T1 on behavior at T2. However, showing that two treatments at T1 lead to different behavior in a standard test at T2 does not allow one to distinguish effects on encoding, that is, on how well the information was stored in the first place, from effects on retention. This theoretical distinction explains why many investigations of the conditions for memory include tests at a variety of retention intervals. Two of the possible patterns of data are shown in Figure 7.7. In Figure 7.7a, two treatments at T1 have resulted in the same performance in immediate tests but performance later declines at different rates, that is, initial encoding is evidently the same but retention differs. In Figure 7.7b, immediate performance differs, but it declines in parallel in the two hypothetical groups. Whether this was called a difference in forgetting rate would depend on theoretical considerations, such as whether forgetting should be measured in absolute or relative terms.

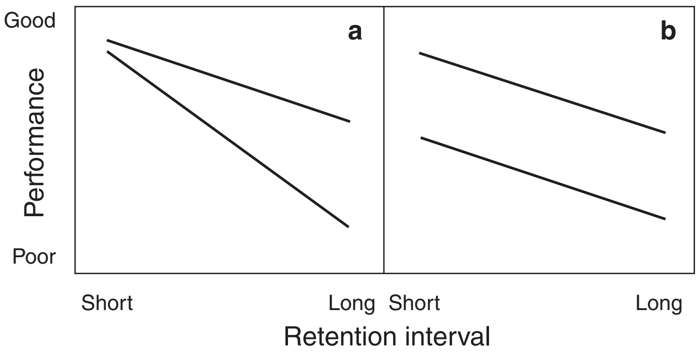


Figure 7.7. Hypothetical forgetting curves showing possible combinations of effects of two treatments on performance after various retention intervals.

7.3.1 Conditions at T1

Amount and distribution of experience.

Grant (1976) trained pigeons to match samples of colors at retention intervals up to 60 seconds long. The birds' exposure to the samples was varied from 1 second up to 14 seconds. The pattern of data, in Figure 7.5, was like that in Figure 7.7b: longer exposure, which presumably produces more complete encoding, led to an equal increment in performance at all retention intervals. The time between entire trials, that is, episodes in which information is presented and then tested, is also important. *Spacing* of trials in which different information is presented, that is, lengthening the intertrial interval (ITI), improves performance. For instance, in delayed matching to sample with colors, pigeons averaged 90% correct with an ITI of 20 seconds but only 73% correct with an ITI of 2 seconds (Maki, Moe, and Bierley 1977). When rats had eight successive trials on a radial maze in one day, performance was worse from the second trial onward than on the first (Figure 7.8). This is an example of *proactive interference,* discussed in Section 7.3.2.

Kind of items to be remembered

Some events, such as those closely related to survival, may be intrinsically more memorable than others (Nairne, Pandeirada, and Thompson 2008). The similarity of the current event to other to-be-remembered events is also important. In studies of human memory, a distinctive item such as a flower name in a list of vehicles is remembered especially well, a phenomenon known as the *von Restorff effect* (R. Hunt 1995). Similarly, when W. Roberts (1980) trained pigeons to match either

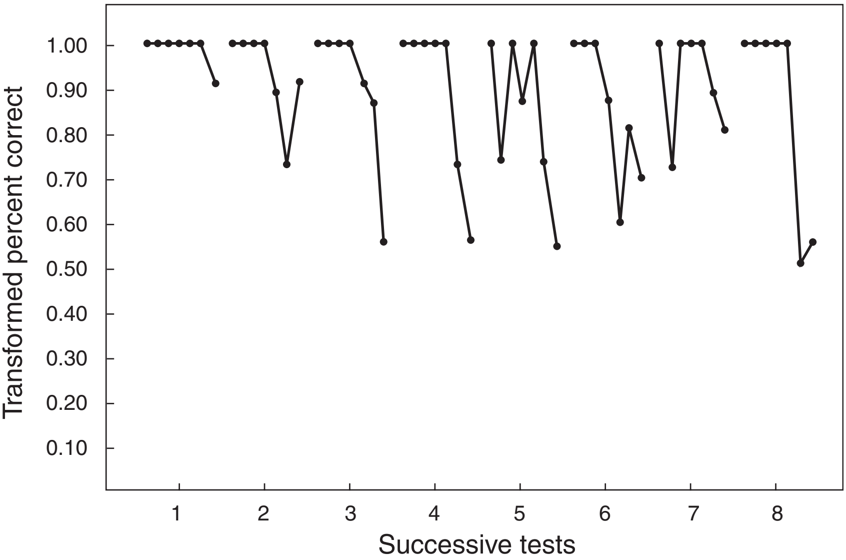


Figure 7.8. Performance (% correct on choices 2–8) on eight successive radial maze tests within the same day, an example of proactive interference. Data within each test are from the seven visits following the first one (which is necessarily always correct). Scores are transformed so that zero is chance. Redrawn from Olton (1978) with permission.

colors or lines and then exposed them to sessions in which a single trial with lines followed every three trials with colors, the birds matched samples of lines more accurately than under control conditions in which line trials were less distinctive. Another effect on memorability in both people and nonverbal animals (monkeys) is the *generation effect;* active participation in generating to-be-remembered items leads to better memory than passive exposure (Kornell and Terrace 2007). An event can be surprising and hence memorable because of previous conditioning; for instance, food is surprising after a CS that has always predicted no food (Wagner 1978; Grant, Brewster, and Stierhoff 1983). Increasing the number of discriminable features of to-be-remembered events improves performance, as in the radial maze versus operant tests of memory. Warningly colored prey (Box 6.3) often have several distinctive features and these may have evolved because they enhance memorability (Guilford and Dawkins 1991; Rowe 1999). For example, bees are bright yellow and have conspicuous black stripes and they buzz.

Divided attention

Having multiple distinctive features may enhance memorability of an object as a whole, but the flip side is what happens to the memorability of a single feature like the bees' yellow color when it is accompanied by other memorable features. Research on divided attention in matching to sample addresses this question. Most experiments on this topic have used pigeons as subjects and color and shape or orientation as the to-be-remembered features, as in Figure 7.9. The essence of such experiments is to ask the pigeon about one feature, for example, "what color was it" or "what shape was it," and compare accuracy on trials with a sample consisting of one feature (or *element*) to accuracy on trials with a compound sample. On the latter trials either element may be tested, so the bird should remember both. With two visual features, pigeons typically match an element more poorly on compound than on element trials, as if any one element is processed less well when the animal divides attention between it and another element (Figure 7.9). Research on divided attention in matching to sample has had to address a large number of possible confounds in findings like those in Figure 7.9, but when they are eliminated the results are still largely consistent with divided attention (Zentall 2005b).

Divided attention effects are not found with all combinations of features (Sutton and Roberts 1998; Zentall 2005b). One feature may completely preempt processing: pigeons can symbolically match samples of sound to visual stimuli, but performance falls to chance when a sample of sound is accompanied by a to-be-remembered visual signal (Kraemer and Roberts 1985). On the other extreme, multiple features may be processed with no interference. Dark-eyed juncos and black-capped chickadees matching the color and/or location of samples on a touchscreen show no divided attention effect for location, although color matching does suffer in both species when location is also being processed (Shettleworth and Westwood 2002). Pigeons, however, can match both the duration and the color or location of a visual stimulus as well as they match each feature alone (Sutton and Roberts 1998), but performance on a more demanding duration matching task does fall when attention must be divided with color or location (Sutton and Roberts 2002). The evidence that location and time memory do not suffer when visual identity is being processed concurrently is consistent with suggestions in Section 7.6 that animals form memories for unique conjunctions of temporal, spatial, and identity information.

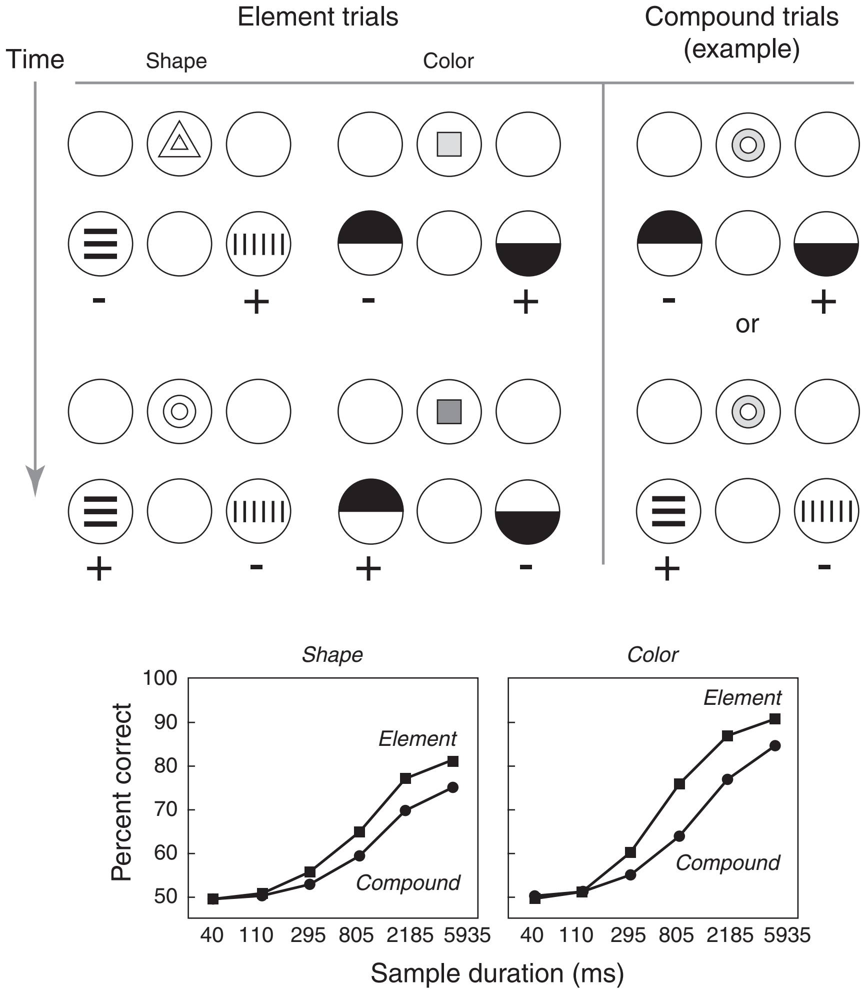


Figure 7.9. Symbolic matching to sample procedure used by Langley and Riley (1993) to test for divided attention in pigeons, together with their results. Two examples of compound trials are shown in which the sample is the same colored shape but memory for the shape (top) or color (bottom) is tested, unpredictably to the pigeon. Data redrawn from Langley and Riley (1993) with permission.

Chunking

As we have seen, several events that have to be remembered at once, as in the radial maze, are better remembered if they are more distinguishable from one another. At the same time, however, large numbers of items are better remembered if they can be grouped into subsets, *chunks* of similar items. For example, people recall more of a long list of words if the words can be grouped into categories such as names of cars, flowers, animals. Pigeons learning to peck several displays in a fixed sequence do so more quickly if the displays are chunked by the experimenter, for example with three colors to be pecked first followed by two patterns (Terrace 1991). Rats behave as if they spontaneously chunk information on a radial maze. Dallal and Meck (1990) exposed rats to a 12-arm radial maze with cheese, chocolate cereal, and pellets of rat chow each on four arms. Rats acquired accurate performance more quickly when the same food was assigned to each arm on every trial than when the locations of the different food types were not predictable from trial to trial. The rats in the former condition chunked their visits by food type, going first to cheese, then cereal, then to the least preferred pellets, but this might have reflected the rat's preferences rather than anything about their memories. To check on this possibility, Macuda and Roberts (1995) tested rats that had learned a maze with fixed food types as in Dallal and Meck's (1990) study by selecting four arms for them to visit at the start of each trial, then allowing a free choice among all 12 arms of the maze. In the whole chunk condition, the four arms selected in the first part of the trial all had the same type of food; in the broken chunk condition, they included arms with all three of the foods. Rats in the whole chunk condition had to remember only one item of information whereas in the broken chunk condition they had to remember all four individual visited arms. As this notion predicts, rats in the whole chunk condition performed more accurately.

The potential for chunking in these experiments was enhanced by providing obvious subsets of items, but monkeys, as well as people, also show evidence of spontaneously chunking remembered information at the time of test. When monkeys have learned to touch a sequence of seven or more simultaneously displayed items in a fixed sequence (a simultaneous chain, see Chapter 10), they typically touch the first few in quick succession, then pause before quickly completing the sequence, as if executing the list in two chunks (Terrace 2001).

7.3.2 Events before and during the retention interval: Interference

Performance at T2 may fall if the retention interval contains events similar to the to-be-remembered target event, an effect called *retroactive interference* (*RI*). An example from habituation is shown in Figure 7.10. The response measured was

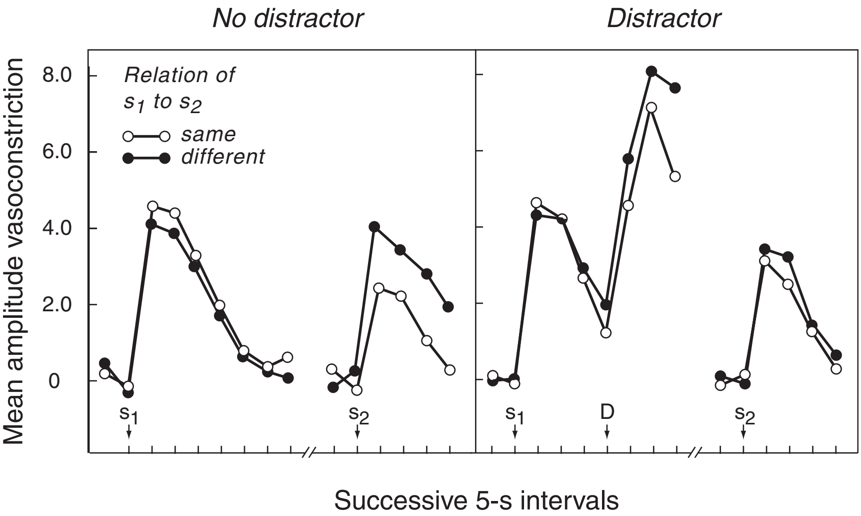


Figure 7.10. Demonstration of retroactive interference produced by a distractor stimulus (D) between successive presentations of a tone to which rabbits are being habituated. Reaction to the tone is measured as the temporal pattern of vasoconstriction in the ear. Redrawn from Whitlow (1975) with permission.

vasoconstriction in rabbits' ears, corresponding to the rabbits' pricking up their ears to a novel sound. Memory for the habituating sound was evidenced in the fact that the rabbits responded less to the second sound in a trial if it was the same as the first sound than if it was different. Interference with memory for the habituating sound was produced by presenting a *distractor* stimulus such as a brief flash of light shortly after the habituating stimulus. In this case, the rabbits apparently forgot the first tone; response to the second tone was undiminished whether or not it was the same as the first one. Comparable effects over longer time courses have been demonstrated in pigeons and monkeys performing delayed matching to sample (Jarvik, Goldfarb, and Carley 1969; W. Roberts and Grant 1978). For example, if the lights in the testing chamber are usually off, turning them on during the retention interval disrupts pigeons' matching (Maki, Moe, and Bierley 1977).

Spatial memory seems less susceptible to interference. For example, taking the rat off the maze or introducing other experiences during the retention interval between the first and last four choices has no effect on performance on a radial maze (S. Roberts 1981). Pigeons performing delayed alternation in a T-maze are also resistant to retroactive interference (Olson and Maki 1983). Similarly, if marsh tits (*Parus palustris*) store two batches of seeds in laboratory "trees," memory for the second batch stored interferes little if at all with memory for earlier stores (Shettleworth and Krebs 1982; see also Crystal and Shettleworth 1994). In contrast, Clark's nutcrackers show clear interference effects on what is probably a more sensitive test, with storage sites close together on the floor of an aviary (J. Lewis and Kamil 2006), perhaps an example of increased interference among more similar memories. Further research would be needed to test the possibility that species and/or memory systems also differ in susceptibility to interference.

In *proactive interference* (*PI*), memory for later events is degraded by memory for earlier ones. Figure 7.8 shows PI between trials: performance declines on successive visits to a radial maze when they are closely spaced in time. PI can also be produced by events within a trial, as when the sample in a delayed matching trial is immediately preceded by a different sample. Proactive interference can build up over a long time. For example, monkeys' accuracy at matching to sample with the same set of stimuli in every session fell over many sessions, but it shot up when a new set of stimuli was introduced (Wright 2006). This may also be another example of the more general beneficial effect of novelty on processing.

Finally, as discussed further in the next section, experiences may interfere with performance without affecting memory per se. A nice example is provided by a study of honeybees (Cheng and Wignall 2006). Bees that learned to find sugar water on the left of a green landmark retained this memory for at least an hour in the absence of intervening experience, but if bees learned to go to the right of a blue landmark during the hour's retention interval, their performance on the first task fell to chance. This does not mean memory was impaired by learning another task, because bees that learned to visit a blue rather than a yellow card for sugar water during the retention interval performed as well on a test of the original task as bees with no intervening experience. Rather, because of response competition bees trained on two tasks with opposite requirements make many wrong choices on the test. If the test with the green landmark was arranged so it was impossible to choose a location to the right of it but only locations above, below, and to the left, performance was nearly as high as before training on the second task of the procedure (Figure 7.11). Of course the results of this study hardly mean that honeybees never forget, but in their natural foraging they may well need memories for several concurrently available nectar sources, and unlike in

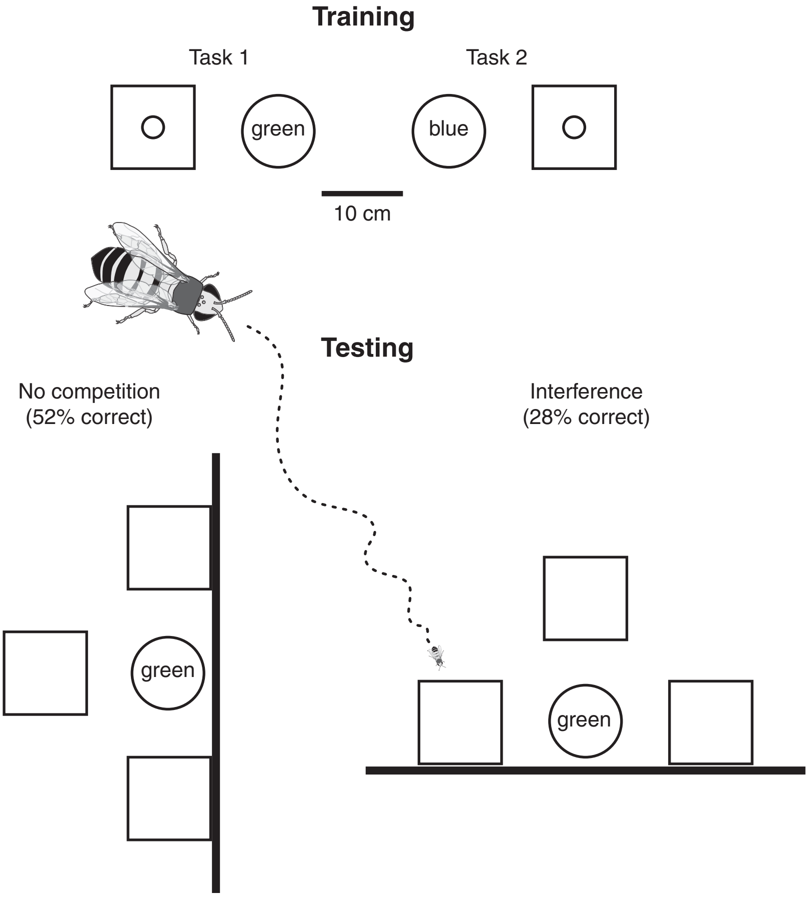


Figure 7.11. Procedure used by Cheng and Wignall (2006) to control the presence versus absence of a competing response from Task 2 during a test of memory for Task 1, learned earlier. In the training phase, the large circles represent cylindrical landmarks, and the small circles are dishes of sugar water. The heavy lines represent the edge of the outdoor table on which the experimental setup was placed. Which of the squares (pieces of red cardboard) a bee landed on indicated its choice.

Cheng and Wignall's (2006) experiment these might not share a spatial context. Box 7.1 describes another situation in which changes in performance over time reflect the presence of several memories.

7.3.3 Conditions at T2: The importance of context

Temporal and spatial context may predict what memories will be useful and therefore ought to be retrieved (Anderson and Schooler 1991). As suggested by the discussion of conditioning to the context in Chapter 4, any and all elements of the external and internal environment present at the time of encoding can provide *retrieval cues* later on (Bouton and Moody 2004). When animals learn first one thing then something incompatible the resulting behavior is a product of both interference and context (Bouton 1993; Bouton and Moody 2004). For example, spontaneous recovery following extinction (Section 4.4.7) reveals that the memory of conditioning is not erased. Rather, animals have two competing memories and evidence one or the other, according to the current context. Immediately after extinction, the temporal context is like that in which extinction took place, but as time passes and both training and extinction are in the past, memory of the original training resurfaces (see also Box 7.1). Another way to show that memory of training is intact is to give noncontingent presentations of the original reinforcer, part of the original training context, just before a test. These reminders tend to reinstate the trained behavior.

Memory for context itself becomes less specific with time. This can have an apparently paradoxical effect: a response that is highly context-specific soon after training later becomes stronger, not weaker, in a novel context. In the example in Figure 7.12, mice that had a single shock in a distinctive chamber gradually developed more freezing (i.e., immobility, evidence of fear) in a novel chamber while showing no forgetting in the original chamber (Wiltgen and Silva 2007; see also Winocur and Moscovitch 2007). It is worth noting that in fear conditioning, animals must be exposed to the to-be-conditioned context for a short time before shock is given, apparently forming a representation of the context to which shock is associated. This is indicated by the absence of learning in the nonexposed group in the right panel of Figure 7.12. The difference between the other groups indicates that it is this representation that becomes less specific over time.

Context includes the time of day at which the to-be-remembered experience occurred. When time of training and time of testing are both controlled for, animals tested at the time of day when they were trained may show better retention than those tested at a different time (McDonald et al. 2002; Cain et al. 2004). Effects of time of day on memory retrieval exemplify the more general phenomenon of *state-dependent learning,* also seen when learning acquired under the influence of a drug is less evident in the drug-free state (Gordon and Klein 1994). At the same time, however, behavior in experiments on memory may change when the context changes for reasons unrelated to changes in the memories being tested (Wilkie, Willson, and Carr 1999; C. Thorpe., Jacova, and Wilkie 2004). For example, animals placed in a new environment may explore it before performing a previously reinforced response, and the resulting delay in responding may wrongly be interpreted as evidence of forgetting (Devenport 1989).

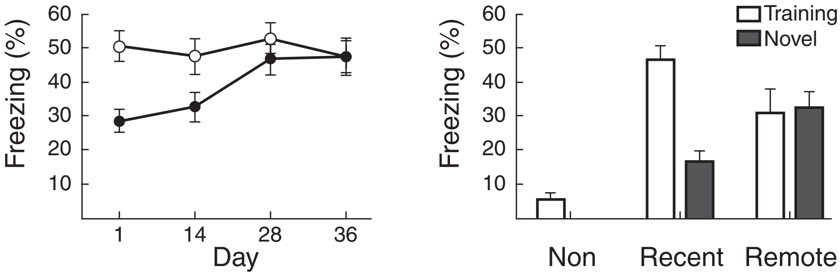


Figure 7.12. Left: proportion of the test spent freezing by separate groups of mice given a single shock in a distinctive chamber and tested at the given retention intervals in the training chamber (open circles) or a novel one. Right: proportion of time freezing in the training or a novel context by groups of mice exposed to the training context either not at all (non), 1 day before (recent), or 36 days before a single shock in the training context. After Wiltgen and Silva (2007) with permission.

7.4 Species differences in memory?

In Chapter 3 of *The Descent of Man and Selection in Relation to Sex,* Darwin (1871) claimed that memory is one of the "mental powers" that humans share with other animals. The behavior of his own dog provided one example. When Darwin returned from his voyage on the *Beagle* after an absence of five years and two days, the dog ran out of the barn when Darwin called and greeted his master as if he had never been away. This and Darwin's other anecdotes suggesting that animals can sometimes remember for a very long time are among the first contributions to a still-growing body of research comparing the persistence and capacity of memory in different species. Given the discussion in Chapter 2, readers should be skeptical that establishing any species differences will be possible, let alone easy. Nevertheless, from the early days of research on animal cognition, there has been a whole series of research programs designed to do just that. Here we review three sorts of tests of the notion that some animals remember things differently from other animals. The first is of mainly historical interest as an illustration of the problems that afflict comparative research on any aspect of cognition. The other two are exemplary ongoing programs of great depth and sophistication, one testing predictions about differences among closely related species with different foraging and social ecologies and the other testing a wide range of species for memory processes shared with humans.

Some examples of long-lasting memories in nature were mentioned earlier in the chapter, but tasks learned in the laboratory can also be remembered for a long time. The effects of simple instrumental training procedures may be retained for months or years (Vaughan and Greene 1984). More remarkably, large numbers of discriminations between complex visual stimuli can be remembered for long periods. For example in one of Vaughan and Greene's (1984) studies of pigeons' discriminations between large numbers of photographic slides, reviewed in Chapter 6, above-chance performance on 160 discriminations (320 slides) was retained for over two years. More recent evidence suggests that pigeons' memory capacity in such a paradigm is actually closer to 800 items (Cook. et al. 2005), and baboons trained similarly over several years learned which response to make to over 3500 pictures (Fagot and Cook 2006). Another example of persistent, large-capacity memory in birds is Clark's nutcrackers' memories for the locations of their buried caches. In the field, these birds bury several thousand caches of pine seeds in the late summer and retrieve them up to six months or more later (Box 1.4 and Section 7.4.2). Nutcrackers performed above chance levels in the laboratory when retrieving 18–25 caches 285 days (9–10 months) after making them. Performance was worse at this retention interval than at 183 days (6 months), a more realistic interval from the point of view of what happens in the field (Balda and Kamil 1992).

Remembering 25 locations for 9 months is not as impressive as remembering 320 slides for 2 years. Does this mean that the excellent memory of food storing birds is a myth, that they are outclassed by ordinary laboratory pigeons? Clearly not. Absolute memory duration is not a meaningful measure when comparing species tested in two such different tasks as those experienced by the pigeons and the nutcrackers. For instance, one involves spatial information, the other two-dimensional visual patterns. Perhaps most important, the food-caching bird has just a brief encounter with each to-be-remembered site, as it pokes its beak into a hole to bury the pine seeds, whereas Vaughan and Greene's pigeons were trained extensively. The pigeons had the first set of slides for a total of 52 sessions, in each of which every slide was shown twice for a minimum of 10 seconds each time. Clearly, the conditions for memory formation differed considerably from those experienced by the nutcrackers. While both sets of data can be taken, along with the story of Darwin's dog, as evidence that animals may have remarkably durable memories, they tell us nothing about whether one animal remembers more or for longer than another.

7.4.1 Comparative tests of delayed responses

The first major research program designed to compare memory in different species in a systematic way was begun by Hunter (1913), using the delayed response task described in Section 7.2. Its purpose was to compare species in "intelligence" by measuring the maximum delay at which performance remained above chance. But this enterprise was beset by the same problems as the comparative studies of successive reversal and learning set reviewed in Chapter 6. As summarized by Maier and Schneirla (1935/1964, 449, Table 30), the early research showed that rats, cats, dogs, raccoons, and five species of primates could all perform correctly without observable orienting responses during the delay, but the maximum delay possible varied drastically among studies. For example, for chimpanzees it ranged between 2 minutes and 48 hours, but rats were hardly worse, with a range between 11 seconds and 24 hours. Obvious differences among the procedures did not seem to account for such variations. Maier and Schneirla (1935/1964, 453) therefore concluded, "differences in results obtained in the various experiments on delayed reaction are artifacts and not measures of a special ability to delay a reaction. As a result, the delayed reaction cannot be regarded as a measure of some higher process." More recent research has not altered this conclusion (Macphail 1982). Comparing species on the shape of an entire forgetting curve, as in Figure 7.13, does not eliminate the problem. Making the task easier or harder for a particular species simply raises or lowers its curve relative to those of other species. The influence of such contextual variables serves to underline Macphail's (1982, 275) conclusion that "delayed response tasks will not provide

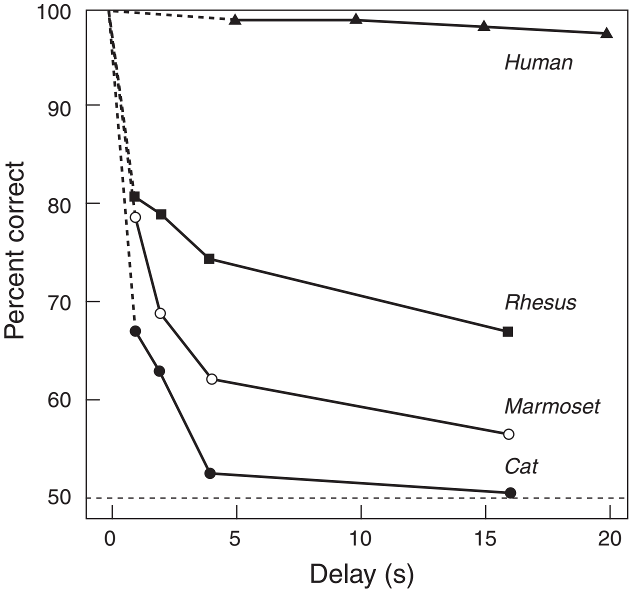


Figure 7.13. Forgetting curves for four mammalian species on a spatial delayed response test. Chance performance is 50% correct. Redrawn from Miles (1971) with permission.

unique rankings of species and cannot be used as a measure of general intelligence." Nor, we may add, of some hypothetical generalized ability to remember.

7.4.2 Spatial memory in food-storing birds

Comparing memory in food-storing and nonstoring species of birds, introduced in Chapters 1 and 2, also involves testing different species in similar situations, so why isn't it just as hopeless a task as attempting to rank species in memory on delayed response tests? What makes it different is that in the ecological or synthetic approach to animal intelligence (Kamil 1988) a profile of species differences and similarities is predicted from ecology and phylogeny, and in the best applications of this approach the species involved are tested in more than one way. Importantly, this includes situations where different patterns of abilities are predicted. Multiple tests of the ability in question are used to be sure that any species ranking is not the product of contextual variables peculiar to one of the tests. Tests of different abilities are used because if, for example, Species A is predicted to have better spatial memory than Species B, and they are never compared on anything other than tests of spatial memory, it is impossible to know whether A outperforms B because it has a specifically better spatial memory, because it has better memory in general, because it adapts better to the laboratory, or for some other reason (Lefebvre and Giraldeau 1996; Shettleworth and Hampton 1998).

A uniquely thorough example of this approach is the program of research on four food-storing corvid species that live in the mountains of the American Southwest (Table 7.1; see Box 1.4; Balda and Kamil 2002, 2006). The star of this show is Clark's nutcracker (*Nucifraga columbiana*), which makes a few thousand pine seed caches every fall and retrieves them throughout the winter and following spring. At the other extreme is the Western scrub jay (*Aphelacoma coerulescens*), a bird of lower elevations that is much less dependent on stored food. Pinyon jays (*Gymnorhynus cyanocephalus*) are intense food-storers but somewhat less so than Clark's nutcrackers; unlike the comparatively solitary nutcrackers they form large flocks. Mexican jays (*A. ultramarina*) are also quite social but are only moderate storers (Balda and Kamil 2006). The latter three species are thought to have diverged from a common ancestor that migrated into North America from the south, whereas the ancestors of nutcrackers, more closely related to European corvids, came across the Bering Strait. Nutcrackers and pinyon jays have some convergently evolved morphological adaptations for gathering and transporting seeds that the other two species lack. Research on the spatial memory of these four species was designed to test the hypothesis that

Table 7.1 Relative ranks of four corvid species studied by Balda and Kamil (2006) on food storing, hippocampus, and performance in tests of memory

	Clark's nutcracker	pinyon jay	Mexican jay	scrub jay
reliance on storing	1	2	3	4
relative hippocampal vol.	1	2	3	2
cache retrieval accuracy	1	2	?	3
radial maze performance	1	1	2	2
spatial delayed nonmatching	1	2	2	2
color delayed nonmatching	2	1	1	2

Same rank indicates no significant difference was found between the given species on the test in question.

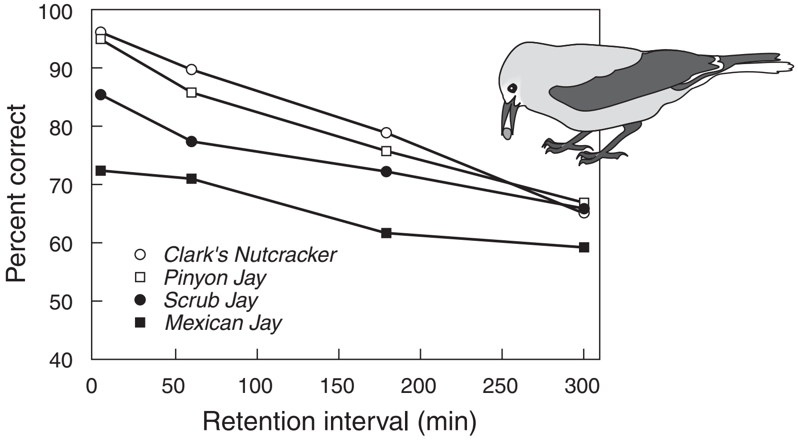


Figure 7.14. Performance of four species of corvids on a radial maze–like task as a function of retention interval between the first and last four choices. Retention intervals were randomly intermixed, unpredictably to the birds. Percent correct is based on the last four choices. Redrawn from Kamil, Balda, and Olson (1994) with permission.

reliance on stored food predicts duration and/or capacity of spatial memory. In tests ranging from retrieving stored food in the laboratory to delayed spatial nonmatching to sample in an operant chamber, the ranking of species fairly consistently supports this hypothesis (Table 7.1; Balda and Kamil 2006).

On a radial maze–like task in which the birds had to remember sites in a large room for up to 24 hours, nutcrackers and pinyon jays consistently performed better than birds of the other two species. However, as shown in Figure 7.14, their advantage was greatest at the shortest retention intervals. This is surprising because the species are assumed to differ in the wild in their ability to retain information for a very long time. This might mean that the species differ in initial processing of spatial information rather than ability to retain it (Kamil, Balda, and Olson 1994). However, differences in initial processing alone should be reflected in forgetting curves that are parallel rather than converging, as in Figure 7.5. In any case, the fact that species differences consistent with the requirements for spatial memory in the wild appear in situations other than food-storing tells us something about the organization of memory in these birds. The mere fact that they retrieve their caches a remarkably long time after making them need not mean they excel in memory in any given way. Encoding spatial information more accurately (Gibson and Kamil 2005), retaining it longer, or being able to keep more items of spatial information in memory could all, singly or together, be selected because they enhance the ability to retrieve stored food. Noncognitive modifications could play a role, too, such as more efficient food storing behavior or ways of storing that make cache sites more memorable.

Nutcrackers, pinyon jays, and scrub jays were also trained on spatial delayed nonmatching to sample in a two-key operant chamber (Olson et al. 1995). The retention interval was increased gradually for each individual as long as it was performing above a standard criterion level so that each bird had the opportunity to show the best it could do: birds with good memory had the retention interval increased faster than birds with poor memory. The nutcrackers performed vastly better than any of the other three species, which performed similarly to each other

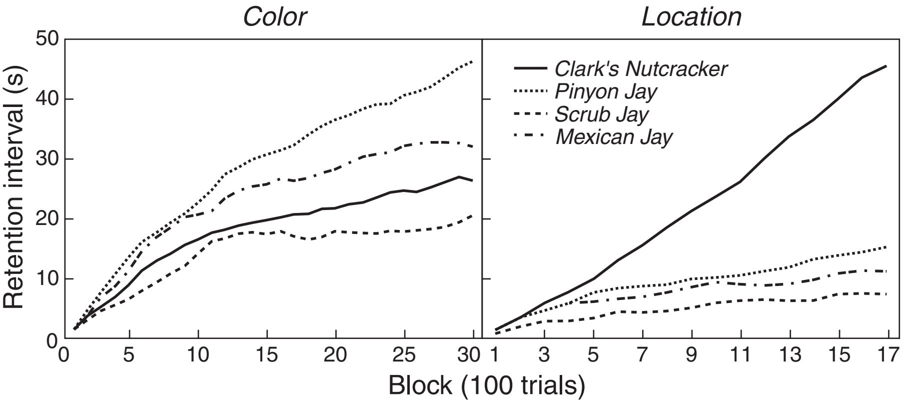


Figure 7.15. Performance of four corvid species on operant delayed matching with samples of color or location. Performance is retention interval attained as a function of trials when the retention interval was increased for each bird whenever it performed above a criterion level. Redrawn from Olson et al. (1995) with permission.

(Figure 7.15). The Clark's nutcrackers also remembered more items than scrub jays in an operant test of spatial memory capacity (Olson 1991). Importantly, in one test of whether the observed species differences are specific to spatial memory or reflect some contextual variable that favors nutcrackers and pinyon jays, the same birds were trained on delayed nonmatching with colors (Olson et al. 1995). Pinyon jays and Mexican jays rather than nutcrackers learned this task fastest and achieved the longest retention intervals (Figure 7.15).

The four species studied by Balda and Kamil differ in sociality as well as reliance on stored food. Because sociality is thought to require its own suite of cognitive adaptations (Chapter 12), the relative performance of the same species can be predicted for rather different cognitive tests. For example, because pinyon jays and Mexican jays travel in groups while caching, they were predicted to be better able than nutcrackers to remember the locations of caches they saw a conspecific making. Indeed, after a two-day retention interval, pinyon jays and Mexican jays retrieved caches they observed as accurately as caches they made themselves, but nutcrackers did not (Templeton, Kamil, and Balda 1999). Pinyon jays also outperform scrub jays on a test of transitive inference, which is thought to require the same ability used in learning a social hierarchy, an ability needed by pinyon jays but not scrub jays (see Chapter 10; Bond, Kamil, and Balda 2003).

The prediction that reliance on food storing is associated with exceptional spatial memory has also been tested with some European corvids and with birds of the family *Paridae,* the chickadees and titmice (Shettleworth 1995). Comparative studies of parids' spatial memory have not revealed species differences so large or so consistent as those among corvids, perhaps reflecting the fact that cognitive and neural mechanisms underlying the ability to retrieve stored caches differ in different groups of species. Food storing has evolved independently in parids and corvids, so perhaps it has recruited somewhat different mechanisms. Also corvids show the most long-term storage in the wild, so they might show more extreme species differences in memory (Brodin 2005). However, one consistent finding across parids and corvids is that in a variety of laboratory tests food-storing species tend to remember spatial cues better than and choose them in preference to color and/or pattern cues, whereas nonstorers treat the two classes of cues about equally (Shettleworth and Hampton 1998; Shettleworth and Westwood 2002). As discussed in Chapter 2, the general notion that greater use of spatial information in the wild should be correlated with enhanced spatial ability (and a larger hippocampus) has also been tested by examining possible differences between males and females, migratory and nonmigratory species, and in other ways. However, so far only with the four American corvid species do we have such a rich and detailed comparison of ecologically relevant cognitive abilities across such a variety of tasks.

7.4.4 List learning in pigeons, rats, monkeys, and people

The *serial position effect* is a classic observation in studies of human memory: items at the beginning and end of a list are typically remembered better than items in the middle. The typical U-shaped curve describing accuracy as a function of position in the list thus contains both *primacy* (better performance with items at the beginning) and *recency* effects (better performance for items at the end). Because the serial position effect is well established in humans, testing for it in other species is frank anthropocentrism. Nevetheless, comparative work on list learning illustrates how asking a rather nonecological question about more or less arbitrarily chosen unrelated species can lead to important insights into general mechanisms of memory. This is the research of Wright and his colleagues on *serial probe recognition* of visual stimuli in pigeons, monkeys, and people (Wright 2006). In serial probe recognition, the subject sees a series of visual images, the to-be-remembered list, followed after a retention interval by a single probe image. If the probe is the same as an item in the list, the subject is reinforced for making one response, say pecking the right key; if it is different from any item in the list, another response is reinforced. Only one item is probed after each list, so that memory for the first, second, and following list positions is tested in a standard way.

In pigeons, monkeys, and people tested with visual items, recency is evident at the shortest retention interval tested. Recency gradually gives way to primacy as the retention interval lengthens (Figure 7.16). The classic U-shaped serial position curve therefore appears only at intermediate retention intervals. The three species differ, however, in the range of retention intervals over which this dynamic pattern appears. “Long” for pigeons is 10 seconds; for the monkeys, 30 seconds; and for humans it takes 100 seconds for recency to be replaced by primacy. The time scale also depends on the task. Rats tested on the radial maze were required to discriminate between one of four arms already entered and an unentered arm show the same sort of dynamic serial position curves displayed in Figure 7.16, but over 16 minutes (Bolhuis and van Kampen 1988; Harper, McLean, and Dalrymple-Alford 1993).

A striking feature of the data in Figure 7.16 is that as time passes the items from the beginning of the list are responded to more accurately. For instance, on the first item pigeons are at chance on an immediate test but about 80% correct after 10 seconds. One way to understand this effect, as well as the whole pattern of dynamic changes, is to suggest that at short retention intervals the early items suffer from retroactive interference from the last items, which are still held in primary or short-term memory at that time. Such retroactive interference evidently dissipates rapidly, perhaps as items move from short-term to long-term memory. Storage in long-term memory has been thought to be accomplished by *rehearsal.* In humans rehearsal may be just what the word implies: the person silently repeats the item, thereby giving it longer

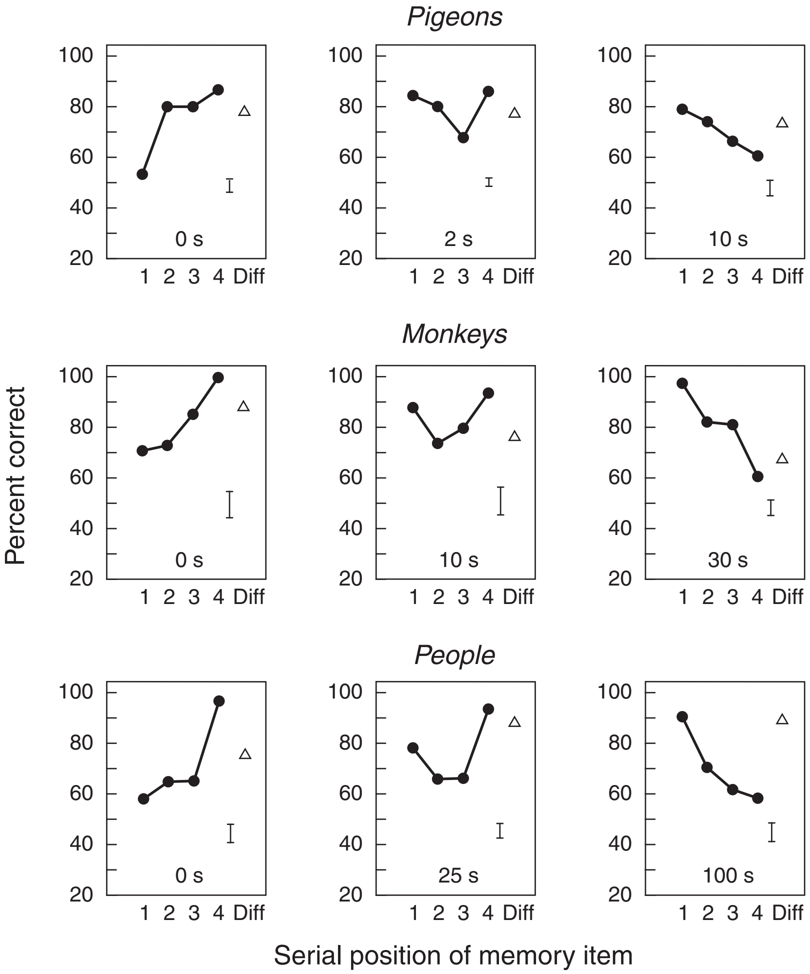


Figure 7.16. Serial probe recognition in pigeons, monkeys, and people with lists of four items as a function of the position of the tested item in the list and the retention interval between the last item and the test (interval indicated in each panel). Triangles are accuracy of indicating "different" on trials in which the probe was an item that had not appeared in the just-presented list. Small vertical bars are standard errors for tests of positions 1–4. Redrawn from Wright et al. (1985) with permission.

exposure. The importance of rehearsal for long-term storage can be demonstrated by inserting *distractors* between items, curtailing rehearsal by making the subject process new material, as in the example in Figure 7.10.

The straightforward notion of rehearsal does not explain the emergence of a primacy effect because performance on the early items improves in absolute terms as time passes. If the items were available to be rehearsed at the shortest retention intervals, they should have been recognized at this retention interval. In addition, because photographs of kaleidoscope patterns were used for the people, they were presumably no better off than the pigeons and monkeys in terms of being able to name and verbally rehearse the to-be-remembered items. To show more directly that the serial position effect in humans can be dissociated from effects of rehearsal, Wright and colleagues (Wright 1989; Wright. et al. 1990) turned to testing the effects of the interval between successive items in the list, *the interstimulus interval* or *ISI*. People perform better with verbal material as the interstimulus interval is lengthened, presumably because there is greater opportunity to rehearse each item as it comes along. On this reasoning, the effect of interstimulus interval should depend on the items being verbally rehearsed. As this idea predicts, people who had learned names for a set of kaleidoscope patterns later performed better on list learning with those patterns and showed a prominent interstimulus interval effect, lacking in a control group also preexposed to the patterns but without learning names for them. Nevertheless, both groups had similar serial position functions, with sharp primacy effects. These findings, like the data from other species, indicate that rehearsal in the sense of verbally repeating the name of an item cannot be the general cause for the primacy effect. As an example of the comparative study of cognition, this research is unusual because it started from an anthropocentric question (do other species show serial position effects like people?) but wound up answering a general question about memory mechanisms by making people behave like nonverbal animals.

Studies of rhesus monkeys' memory for lists of sounds also suggest that rather than rehearsal, dynamic serial position curves reflect the intrinsic time courses of retroactive and proactive interference (RI and PI) among items within a list. Remarkably, serial position curves for auditory lists change with retention interval in the opposite way to those for lists of visual items even when both are tested similarly. This within-species difference in the serial position curve, like the cross-species differences, apparently reflects a quantitative difference in common mechanisms rather than a qualitative one. PI is strongest immediately after a list of sounds is presented and dissipates with time while RI increases (Wright and Roediger III 2003; Wright 2006). Why this should be is somewhat mysterious, but functionally it means that if a monkey is forming a memory for a natural sequence of multimodal events, either the auditory or the visual component of each memory will always be available although the other may be temporarily suppressed.

7.5 Mechanisms: What is remembered and why is it forgotten?

Nowadays studying the mechanisms of memory most often means studying neural and molecular mechanisms, but ultimately of course the findings must explain behavior. In this section we look at some memory mechanisms that have been addressed with primarily behavioral studies. An important historical theme is whether memories consist simply of the persistence of the neural activity that occurs when events are perceived, that is, *stimulus traces,* or whether the direct effect of experience is transformed in some way for storage in memory. Similarly, is forgetting the passive fading of a trace or a more active process? Finally, how do memories sometimes become more stable with time, in the process of consolidation?

7.5.1 Retrospective and prospective coding

A stimulus trace is a *retrospective code*. Intuitively, performance based on stimulus traces results from mentally "looking back" (retro-specting) at recent traces. In a *prospective code,* in contrast, information is transformed at the time of input into some representation of what is to be done at the time of test, that is, the code looks forward or pro-spects. In simple red/green matching to sample, for instance, retrospective coding of the red sample is a trace corresponding to the experience of red, whereas prospective coding of the same sample amounts to an instruction, "choose red on the test." Extensive investigations of the conditions favoring one form of code or the other in short-term or working memory have been done with pigeons in matching to sample tasks. In *many-to-one* matching, each of several samples is associated with the same correct choice. For example, Grant (1982) trained pigeons to choose a red comparison stimulus after samples of red, 20 pecks, or a brief presentation of food, and to choose green following a sample of green, one peck, or no food. When one, two, or three samples were presented in succession before the retention interval, birds performed more accurately with multiple samples regardless of whether they were the same (e.g., two food presentations) or just associated with the same comparison (e.g., one presentation of food and one of the red key).

This finding suggests that samples associated with a common comparison are coded in the same way, that is, prospectively. However, pigeons may not always code information prospectively in matching to sample, let alone in general. Among other reasons, initial learning of any kind requires retrospective coding. It is impossible to form a prospective code without information about what the memory will be used for, so the most primitive memory code must be retrospective. Only when the same items are tested over and over in the same kind of way, either during an individual's lifetime or during evolution, is prospective coding possible. Thus, as with many issues in psychology, the best question is not, "Is coding retrospective *or* prospective?" but rather "*Under what conditions* is coding retrospective and under what conditions prospective?" One condition favoring retrospective coding is the use of highly discriminable samples. For pigeons, colors on the pecking key are much more salient than lines of different orientations. Colors seem to be coded retrospectively even under conditions favoring prospective coding of less discriminable stimuli such as lines (Zentall et al. 1989). Under some conditions, the type of code used appears to switch within a trial (Cook, Brown, and Riley 1985; Brown, Wheeler, and Riley 1989; Zentall, Steirn, and Jackson-Smith 1990).

It is not clear what prospective coding of short-term memories would be good for outside the laboratory because it is hard to think of natural situations in which an animal would repeatedly encounter the same kind of information and its later choices depend on what had happened earlier. Nevertheless, the distinction between prospective and retrospective processes has wider applicability (Wasserman 1986). For instance, prospection can be seen as the ability to anticipate and make plans, issues discussed in Chapter 11. In any case, experiments on time-place learning discussed in Chapter 9 arguably better approximate studies of prospective memory in humans than do studies of coding in working memory. As Thorpe, Jacova, and Wilkie (2004) point out, in studies of prospective memory with people, subjects are told to remember to do something at a certain time or when a certain cue appears, as in everyday life when making a date to meet for lunch.

7.5.2 Directed forgetting

One way to test whether memory is a passive recording of a trace or a more active process is to see whether remembering can be brought under stimulus control. People can be told to remember some things and forget others, and such instructions do influence later recall (see Zentall et al. 1997). In *directed forgetting* experiments with nonverbal species, distinctive stimuli inserted into the retention interval play the role of instructions to remember or forget. Such cues are presented after the sample stimuli so they can affect only processing of their memories. But "forget" and "remember" trials may differ in many other ways. For example, if there is never a test of any kind after a cue to forget, that cue will signal absence of reinforcement. The animal may therefore stop attending to the keys until the next trial and behave as if not remembering the sample when memory is unexpectedly probed on "forget" trials. For such reasons, most early tests of whether memory processing can be brought under stimulus control were inconclusive (Zentall et al. 1997).

In tests of directed forgetting with human subjects, people are typically given several items of information and told which to remember; implicitly, this means forget the others. A way of giving pigeons these instructions is diagrammed in Figure 7.17 (Roper, Kaiser, and Zentall 1995). The bird's memory is always tested; what varies from trial to trial is whether the test is of memory for the first of two stimuli presented (a color sample stimulus) or the second (a sample for a symbolic matching test). The appearance of one of the symbolic matching samples, the dot or circle in the example, in effect tells the bird it can forget whether red or green was just presented. With this procedure pigeons do perform worse when memory for the first sample is probed after a forget cue than after a remember cue (Figure 7.17, bottom), apparently reallocating processing from one sample to another.

7.5.3 Consolidation and reconsolidation

Since the time of the ancient Greeks, people have realized that new memories need time to stabilize, reflecting a process known as *consolidation* (Dudai 2004). Two separate consolidation processes are now recognized at the neurobiological level. Cellular or *synaptic consolidation* takes place in the first minutes to hours after learning and depends on protein synthesis, a universal property of memory acquisition in nervous systems. In mammals, memories dependent on the hippocampus undergo a longer term or *systems consolidation* lasting days or even years during which they become represented outside the hippocampus (see Winocur and Moscovitch 2007). As these characterizations indicate, nowadays consolidation—in nonhuman species, at least—is most often studied via manipulations of the nervous system (see Dudai 2004), but behavioral studies, including some with with humans (Wixted 2004), also provide evidence for it.

In one example with mice, (Boccia et al. 2005) the target memory was acquired in a single trial of *step-down avoidance learning* (notice the irrelevance of the distinction between "memory" and "learning" typical of this kind of work). In this task an animal is placed on a small platform elevated above an electrified grid floor. Because the animal is shocked when it steps off, even after a single trial it tends to stay much longer on the platform than a naive animal, and it may retain the memory of the shock for days. The mice spent five minutes in a novel open field with small holes in the floor that mice investigate by poking their noses in ("hole board") either immediately after one trial of avoidance training or three hours later (Figure 7.18). When placed on the platform in the avoidance apparatus one, two, and three days later, the mice exposed to the hole board immediately after original learning stepped down nearly as quickly as unshocked mice, as if they had no memory of the shock. Learning about the novel environment evidently prevented consolidation of memory for the avoidance task. Mice that experienced the hole board three hours after learning all stayed on the platform for the entire five minute test, as did controls unexposed to the hole board (Figure 7.18) Thus here memory is consolidated within the first three hours. What

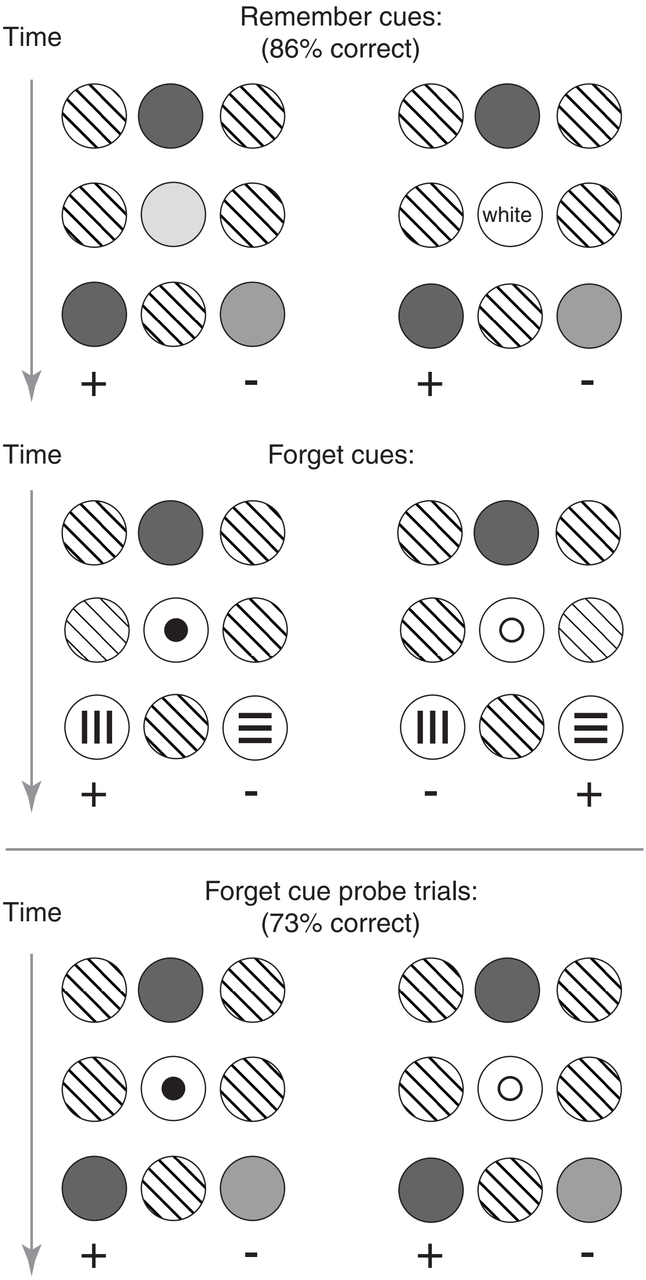


Figure 7.17. Examples of trials in the directed forgetting procedure of Roper, Kaiser, and Zentall (1995). The "forget" cues (small white and black disks) are themselves samples for a subsequent symbolic matching test. Redrawn from Roper, Kaiser, and Zentall (1995) with permission.

interferes with consolidation is not experience of the hole board per se but the new learning it instigates. Mice well habituated to the hole board and then placed on it immediately after avoidance training showed no decrement in memory. Izquierdo and colleagues (1999) report parallel findings with rats. These authors also found that

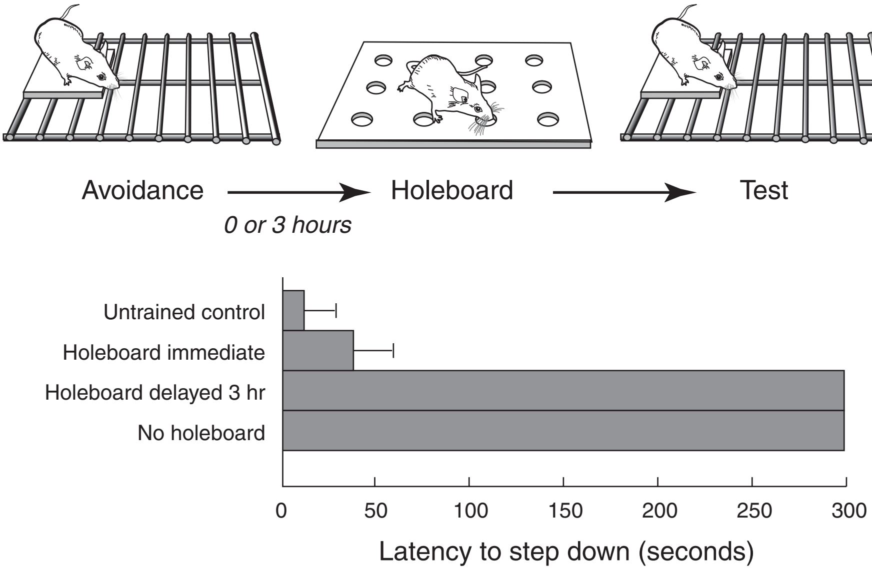


Figure 7.18. Exposure to a novel environment (the holeboard) prevents consolidation of fear memory in mice. Procedure and results of the experiment described in the text (Experiment 1 Boccia et al. 2005) adapted with permission. A longer latency to step onto the grid in the test indicates greater fear. A further control showed that for immediate exposure to abolish fear memory as shown, the holeboard must be novel.

consolidation of memory for the open field is not disrupted by avoidance training, suggesting that it is consolidated more quickly.

The discussion so far seems to suggest that synaptic consolidation is a one-time event, but to the contrary recently formed memories sometimes become labile again when they are retrieved and require *reconsolidation.* In a continuation of the study shown in Figure 7.18 memory for shock was tested 24 hours after training; no shock was given. Then the mice were exposed to the hole board for the first time either immediately or three hours later. Experience on the hole board disrupted memory when it occurred immediately after the test but not three hours later. When mice exposed to the hole board immediately after the memory test were later exposed to noncontingent shock, that is, in a reactivation treatment, they still behaved as if having lost their memories. These findings suggest that on the first test, a day after training, the apparently consolidated memory returns to the same labile state as immediately after training. Whether this is strictly true, whether susceptibility to reconsolidation lasts indefinitely, whether it characterizes all sorts of memories, and related questions are the subject of lively debate and much research, most of it using neurobiological methods (Tronson and Taylor 2007).

7.6 Memory and consciousness

In traditional studies of memory, consciousness is not an issue. Memory is inferred when a creature's behavior at one time (T2) is influenced by experience at an earlier time (T1), as when a mouse is slow to step onto a shock grid again or a person recalls a word from a list. But recent years have seen increased interest in aspects of human memory linked to states of consciousness. Examples include explicit (conscious) as opposed to implicit (unconscious) memory, episodic versus semantic memory, remembering an event as opposed to merely knowing that it happened, and awareness of the strength of one's own memories (metamemory). Perhaps inevitably, researchers have looked for evidence of these processes in other species, partly because "animal models" promise better understanding of their neurobiology. But even if a particular memory process in humans is accompanied by a distinctive subjective experience, researchers testing other species can measure only nonverbal behavior, that is, what the cognitive process in question allows animals to do but not how it feels. The issue therefore becomes the extent to which other species show behavior that is *functionally similar* to that of humans, in the mathematical sense of changing similarly with independent variables (Heyes 2008; Hampton 2009). This is essentially no different from showing that basic memory processes are the same across species, as in the comparative study of serial position effects (Figure 7.16).

As an example of memory processes accompanied by different subjective experiences, consider the distinction between implicit and explicit memory in humans. *Implicit memory* is memory without awareness; *explicit memory* is memory we are aware of in that we can report on it verbally. Some of the now-classic demonstrations that normal adults reliably form memories they are unaware of come from studies of word fragment completion (e.g., Tulving, Schacter, and Stark 1982; Tulving 1985; Schacter 1995). People are shown a few letters of a word and asked to fill in the blanks, as in *_s_s_in* (for *assassin*). Subjects are more successful if the fragments can be completed as words they have recently studied for an unrelated test, even though they may not recognize the completed items as ones they saw recently. Conscious recognition (explicit memory) and implicit, nonconscious memory or *priming* can be dissociated in at least three ways (Tulving 1985). First, individual subjects do not necessarily explicitly remember the same items that show priming; surprisingly, explicit and implicit memory are statistically independent. Second, priming and explicit memory may decay over different time courses (Figure 7.19). Third, some brain-damaged patients with little or no explicit memory for new experiences show normal priming. Similar effects with material such as line drawings of objects

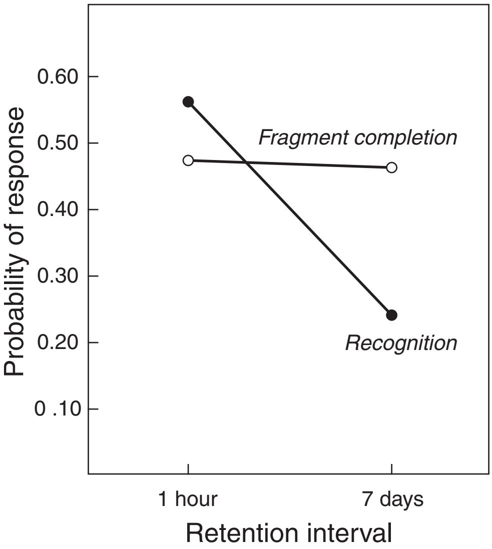


Figure 7.19. Dissociation of word fragment completion and explicit recognition of words presented under the same conditions. Redrawn from Tulving, Schacter, and Stark (1982) with permission.

suggesting that priming with words is but one manifestation of a more general unconscious *Perceptual Recognition System* (or PRS, Tulving and Schacter 1990), perhaps an evolutionarily primitive memory system (Tulving 1995). This hypothesis suggests that animals should also show priming in memory, a notion tested so far in only one experiment (Brodbeck 1997).

The next two sections summarize the more substantial and sometimes controversial research asking whether nonhuman species share other memory processes that are accompanied by distinctive states of awareness in humans, namely metamemory and episodic memory. This is our first extended discussion of some key issues prominent in comparative research on other anthropocentric topics such as physical understanding (Chapter 11) and theory of mind (Chapter 12). These issues are of two kinds, methodological or practical and theoretical. Methodological issues surround deciding what constitutes functional similarity. This is easiest when the process under study is well understood in people, especially when human subjects and other species can be given the same nonverbal tests, as in the comparative study of serial position effects (Section 7.4.3). Even when they cannot, the distinctive procedures and patterns of data providing evidence for the given process should be well defined to begin with. Ideally a variety of tests is available, allowing researchers to seek converging evidence from multiple situations. When instead the process under study is more familiar in folk psychology than in research laboratories, appropriate tests for nonhuman species may not be easy to agree on and how to interpret the results even less so. For example (Chapter 11), most tests of what physical understanding (if any) underlies primates' or birds' use of tools are based more on folk psychological intuition about what people would do in similar circumstances than on actual data. And when experiments are designed to collect such data, they can have counterintuitive results (Silva and Silva 2006).

The principal theoretical issue is that by itself functional similarity between human and animal behavior (or behavior of any two species) is not necessarily decisive evidence for a common underlying process. As with the nut dropping crows in Chapter 1, functional similarity can have multiple possible causes. Consistent with Morgan's Canon (Chapter 1), evidence that some process involving consciousness, understanding, or the like underlies behavior generally consists of evidence eliminating or rendering unlikely the possibility that it results from simpler mechanisms of learning and behavioral control. The latter can be referred to as publicly observable causes, in that behavior is predicted from external cues without the assumed mediation of some unobservable cognitive state (a private cause of behavior, Hampton 2009). The most powerful experimental designs for distinguishing public from private causes place predictions from candidate processes into opposition (Heyes 2008). But even when data are more consistent with a private cause, it is a final theoretical leap to the conclusion that functionally similar behavior reflects the same private cause in different species. One twist here is that students of human cognition are increasingly coming to appreciate that our own accounts of what we do as resulting from conscious thought and rational decision making may in fact be after-the-fact explanations of reactions to simple cues of the sort that other species might also respond to (Koriat, Hilit, and Nussison 2006; Carruthers 2008).

7.6.1 Metacognition

People tend to know how well they remember things. Such *metamemory* has two functions, monitoring memory strength and controlling information-seeking. For example, metamemory allows someone decide whether he remembers the way to a friend's house or needs to consult a map. *Metacognition* additionally includes knowing how well one is able to make perceptual discriminations, as in "I'm sure that green matches the curtains." Formal tests of metacognition require both a primary memory or perceptual discrimination task and metacognitive reports. The metacognitive reports should reflect accuracy on the primary task, as they tend to in tests of human subjects (Nelson and Narens 1990; Metcalfe and Kober 2005).

Because the function of metacognition seems to be facilitating efficient behavior, it might be shared by nonhuman species, and indeed, since the late 1990s researchers have tested for it in pigeons, rats, monkeys, chimpanzees, and a dolphin (J. Smith, Shields, and Washburn 2003; Terrace and Metcalfe 2005; Hampton 2009). However, on some interpretations metacognition entails higher-order representation because cognitive processes are themselves being represented, and this makes its presence in nonhuman species very unlikely (Carruthers 2008; see also Penn, Holyoak, and Povinelli 2008). In that people feel aware of their own memory strength or perceptual certainty, metacognition in humans also involves phenomenal consciousness (Koriat 2007). These features of metacognition mean that purported demonstrations of it in other species have attracted a good deal of critical scrutiny.

Hampton's (2001) experiment

We begin with a test of metamemory in rhesus macaques (Hampton 2001) that provides perhaps the strongest evidence to date that animals can respond to private cues predictive of accuracy on a memory test. Two monkeys performed on a four-alternative delayed matching to sample procedure with an extra step (Figure 7.20). At the end of the retention interval, before the sample and distractors, one or two symbols appeared. On two-thirds of trials, two symbols gave the monkeys a choice between taking the memory test and escaping from it. Choosing to take the test played the role of a person's reporting "I know I remember the sample on this trial." Completing the test correctly was reinforced with a peanut, but taking it and failing got nothing, whereas escaping was reinforced immediately with a piece of monkey chow, less preferred than the peanut. Assuming they prefer chow for sure to a peanut with less than certainty, monkeys with metamemory should escape more often the weaker their memories. Such animals should also perform less accurately on the one-third of memory tests they were not allowed to escape than on tests they chose because these "forced trials" include trials with poor memory, which the animal would have escaped if it could. Of course, if such forced trials were comparatively rare, animals might perform poorly on that account alone, that is, because of generalization decrement, so they were mixed randomly with choice trials throughout (but see J. Smith, Shields, and Washburn 2003; J. Smith et al. 2006).

In effect, the procedure diagrammed in Figure 7.20 reinforces animals for using some correlate of memory strength as a discriminative stimulus and at the same time, in the forced trials, potentially verifies that this cue is being used. But clearly a number of potential publicly observable cues could directly predict success on the memory test. An obvious one is the length of the retention interval. Animals could certainly learn that after a long delay escaping is more profitable than taking the memory test, although at first glance it is not clear how use of this cue could result in differences between chosen and forced memory tests. In any case, Hampton's study was designed so that monkeys could not use delay as a cue because they were trained initially with a

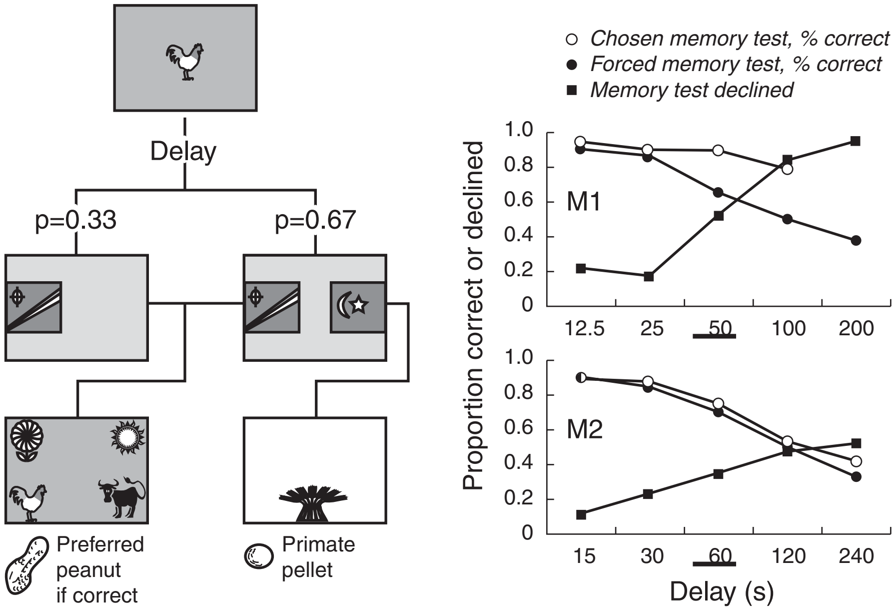


Figure 7.20. Procedure and data from the test of metamemory in monkeys by Hampton (2001) described in the text. In the left panel, each square represents what the monkeys saw at the given stage in a trial, from top to bottom. For example, the rooster at the top is a sample stimulus, and the left most panel in the middle row would be a forced memory test. The two panels on the right show data from two monkeys, M1 and M2.The initial training delay is underlined .

single moderate retention interval at which they were about 70% correct on forced memory tests (Figure 7.20). In contrast, when escaping was available both monkeys were over 80% correct on memory tests they did not escape, that is, they behaved as if reporting fairly accurately on the strength of their memories. To address the possibility that the monkeys' behavior, motivation, or distractions during the retention interval were used as public cues predicting success on the memory test, Hampton then manipulated memory directly by the clever expedient of occasionally omitting the sample. Now, when the monkeys could have no memory of a recent sample, escaping immediately increased dramatically. Finally, the retention interval (RI) was varied across values both shorter and longer than the one the monkeys had been trained on. Again the results were consistent with the animals assessing their memory strength on a trial by trial basis (Figure 7.20). The longer the RI, the worse they did on forced tests, the more they escaped, and the more matching accuracy on chosen tests exceeded that on forced tests. Moreover, this pattern of data appeared within the first 100 such trials.

These findings imply that the monkeys are responding to some private cue that predicts success on the test of memory, and in that sense they are aware of the strength of their memories. But whether this cue shares any of the subjective qualities of a person's awareness of having a strong or a weak memory is impossible to say. The monkeys' behavior does not necessarily entail a higher-order representation, that is, *meta* cognition in the strictest sense (Carruthers 2008). It might, for example, be based on the vividness of a mental image of the sample (Hampton 2005).

Confidence ratings

Metacognitive judgements are sometimes expressed after completing a test, as in "I aced that exam!" Such confidence ratings have been captured in operant tasks by requiring animals to make an additional choice after completing a primary test of memory, in effect rating their confidence in whether they were correct. The "high confidence" option is reinforced if the animal was correct but not otherwise; the "low confidence" option always gives a mediocre reward. Rhesus macaques respond as if having metacognition in such tasks, with choice of the high confidence icon positively correlated with accuracy on the test of memory (Kornell, Son, and Terrace 2007; see also Shields et al. 2005). Consistent with the possibility that this response expresses a subjective sense of memory strength, monkeys transferred appropriate choice of high versus low confidence responses from a series of two perceptual discrimination tasks in the same apparatus to a memory task. This and other such examples of transfer (Shields et al. 2005; Washburn, Smith, and Shields 2006) reveal that the metacognitive reponses must be mediated by something common to all the tasks, but it is not necessarily the subjective feeling of certainty emphasized by Smith and colleagues (e.g., J. Smith, Shields, and Washburn 2003; J. Smith and Washburn 2005; Beran et al. 2006). A strong candidate for a public cue is some feature of the monkeys' own behavior such as response latency in the primary task (Son and Kornell 2005) or expectation of reinforcement, an implicit but not explicit index of memory strength. Indeed, human subjects' metacognitive judgements may be also based on such factors (Metcalfe and Kober 2005; Koriat 2007).

Information-seeking: Metamemory or behavioral conflict?

In everyday life, we often employ metamemory implicitly in the control of information-seeking, as when feeling it's necessary to look in the phone book before dialing. Rhesus macaques were tested for such an ability with a naturalistic task in which they watched the experimenter put a treat into one of four opaque tubes and then had one chance to retrieve it (Hampton, Zivin, and Murray 2004). In preliminary trials they learned that with a little effort they could peer into the tubes to locate the reward before choosing. On probe trials with baiting done behind a screen, monkeys peered down the tubes before choosing more often than when they had seen the tubes baited. Looking increased their rate of success over that on trials on which they chose a tube without looking first. Most importantly, they began looking appropriately right away, before they could have learned to use the screen as a discriminative stimulus. Similar behavior is shown by apes (chimpanzees and orangutans) as well as children (Call and Carpenter 2001), but it is more difficult to demonstrate in capuchins, a species of new world monkey (Basile et al. 2008; Paukner, Anderson, and Fujita 2006). Analogously, in a difficult serial learning task rhesus monkeys chose costly "hints" early in learning new lists but not later on (Kornell, Son, and Terrace 2007).

Unlike in other procedures discussed so far, in the tubes task the opportunity to make the metacognitive response occurs simultaneously with the test. Therefore, the animals' behavior could reflect competing tendencies among responses learned to currently present cues (Hampton 2009). With baiting visible, monkeys have acquired a strong tendency to pull the tube that has just been baited. Looking into one or more tubes and then pulling was also specifically trained, but because it is reinforced only after a delay, looking is not such a strong response as pulling when the baited tube is known. But the tendency to

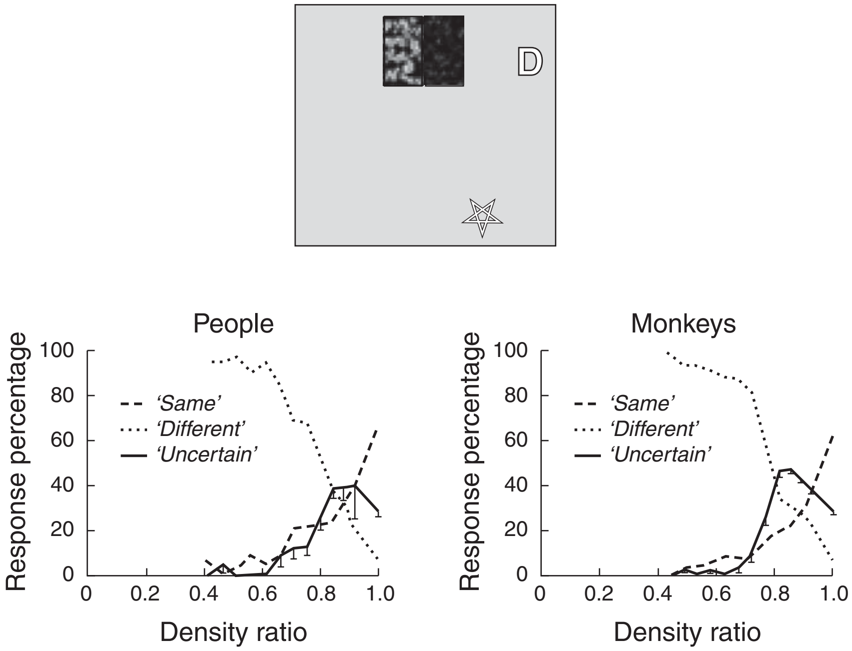


Figure 7.21. Display used to test metacognition in monkeys and people. If the two rectangles at the top of the screen had the same pixel density, touching them was rewarded; if they were different, touching the D was rewarded. Touching the star signified "uncertain" and led to an easy trial after a short delay. The lower panels show average data from 6 people and two rhesus macaques. Adapted from Shields, Smith, and Washburn (1997) with permission.

pull a specific tube is weak when the tubes are presented after an unseen baiting, so the looking response is expressed.

Several other tests of both metamemory and perceptual certainty share with the tubes task the property that a metacognitive "escape" or "uncertain" response is presented simultaneously with the test of cognition (J. Smith et al. 2008; Hampton 2009). Some of the first tests of animal metacognition to be reported involved difficult perceptual tasks in which the animal classified stimuli as bright or dim, high or low, or the like (see J. Smith, Shields, and Washburn 2003). A third "uncertain" option was presented along with the two response options associated with the two stimulus classes. The uncertain response, leading to a delayed or otherwise reduced reinforcement, was usually chosen most when the stimulus to be classified was near the threshold of discriminability. An elegant feature of some of these studies was that human subjects were given the same tests and showed the same pattern of data as the other species tested (e.g., Shields, Smith, and Washburn 1997; Shields et al. 2005). Figure 7.21 shows an example from a diffucult perceptual task (Shields et al. 1997). When people choose the "uncertain" option in such studies, they say they experience a feeling of uncertainty, but whatever the subjective states of the animals here, behavior consistent with metacognition in these tests can be completely accounted for in terms of learned contingencies and the resulting competing response tendencies (J. Smith et al. 2008).

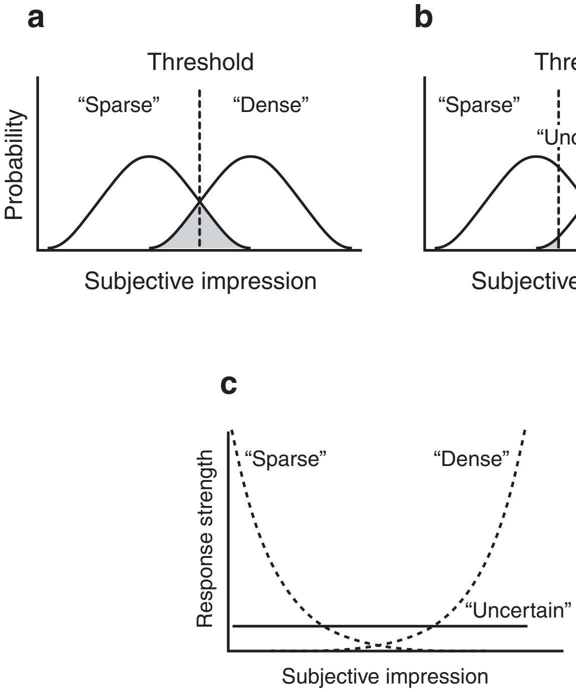


Figure 7.22. Signal detection analysis of a difficult perceptual task. a. Subjects forced to classify the density of pixels as "sparse" or "dense" set a criterion in the middle, but because their subjective impressions of the stimuli overlap, they will inevitably make the proportion of errors indicated by the shaded areas. b. When subjects are allowed an escape or "uncertain" option, using it in the region where the distributions overlap decreases the proportion of errors in trials they choose to complete. c. The response strengths for the three options in situation b when escaping is followed by a reinforcer smaller than that given for classifying the stimuli correctly. Panel c after J. Smith et al. (2008) with permission.

Figure 7.22 shows how the argument goes for a difficult perceptual discrimination. As we know from signal detection theory (Chapter 3), stimuli have a range of subjective effects. The more difficult a discrimination, the more these will overlap. With symmetrical distributions and equal reward for classifying all stimuli correctly, the threshold is located as in Figure 7.22a. Inevitably subjects will make errors, corresponding to the shaded areas of the figure. When an escape or "uncertain" response that receives a mediocre reward is available whatever stimulus is present, it will be the strongest response near the threshold subjective value (Figure 7.22c). In this situation, subjects behave as if partitioning the stimulus continuum as in Figure 7.22b, a situation that results in a higher proportion of correct responses on chosen than on forced trials.

Conclusions

As an account of behavior consistent with metacognition, the analysis in Figure 7.22 (developed by J. Smith et al. 2008) applies most directly to perceptual discriminations in which the escape or "uncertain" option is presented simultaneously with the primary task, as in Figure 7.21. For it to be applicable to a metamemory task, memory strength must be treated as a stimulus continuum, but this amounts to assuming animals are sensitive to the strength of their own memories, which is supposedly being tested in the first place. In any case, although there is now a substantial body of data from monkeys, rats, and a dolphin from a variety of tests of metacognition, nearly all of them are subject to interpretation as direct responses to publicly available cues (J. Smith. 2008; Hampton 2009). The chief exception is Hampton's (2001) experiment. It is one of the few in which the metacognitive response was made before the direct cognitive test so that the animal could respond nonrandomly only by consulting some private cue, a situation impossible to arrange in tests of perceptual certainty.

One response to this state of affairs (J. Smith et al. 2008) is to suggest that "true" animal metacognition must be pursued in situations devoid of differential reinforcement for expressing subjective uncertainty. This suggestion flies in the face of the notion that testing animals for an unknown and difficult-to-observe capacity requires a situation in which reward is contingent on using the capacity, as in the study of bats' echolocation discussed in Chapter 3. Another response is to accept that only very limited paradigms can isolate responses to private cues, or at least have done so up to now (Hampton 2009). Animals may behave in the adaptive ways characteristic of creatures with metacognition without any higher order representation. The same may be true of people to a greater extent than is usually appreciated (Koriat 2007). An important implication of the analysis in this section is that blanket terms such as *metacognition* can mislead investigators (e.g Sutton and Shettleworth 2008) into thinking that disparate tests provide converging evidence for a single process when different mechanisms underlie successful performance in each one. For instance, metacognitive responses in perceptual tasks can be accounted for as direct responses to external cues (Figure 7.22), but this account is harder to sustain for some tests of metamemory, and it would seem to be ruled out entirely when the metacognitive response is made before the test of cognition.

In summary, nearly all the data from tests of metacognition to date can be accounted for in terms of learned responses to external, or "public," cues, although they are also consistent with the animals reporting on a subjective state. One suggestion that the former is not the whole story comes from the fact that pigeons do not behave consistently as if they have any metacognitive ability even though they have been tested with both perceptual and memory tasks with tests of metacognition presented before, concurrently with, and after the choices on the primary task (Inman and Shettleworth 1999; Sole, Shettleworth, and Bennett 2003; Sutton and Shettleworth 2008). Since public associative cues, response competition, sensitivity to reinforcement contingencies and other basic behavioral mechanisms are clearly within the grasp of pigeons, these findings suggest that maybe monkeys have access to some additional process. If studies continue to give results consistent with such a species difference one next step will be to discover whether it is characteristic of mammals versus birds, or whether perhaps the birds discussed in the next session can also show evidence of using private cues in tests of metamemory.

7.6.3 Episodic memory

Episodic memory is memory for specific episodes in one's personal past, as distinguished from *semantic memory,* or memory for facts and ideas. For example, memory for the experience of dinner at Luigi's Restaurant last Saturday night is episodic whereas knowledge about what is involved in having dinner at a restaurant in general is semantic. When it was first discussed (Tulving 1972) episodic memory was defined primarily as a memory for a personal experience, that is, what happened, where, and when. Subsequently, supported by evidence that some people with hippocampal damage have semantic but not episodic memory, the definition of episodic memory evolved to emphasize its conscious component, a feeling of reexperiencing the remembered event (*autonoetic consciousness,* Tulving 2002). It is now (Tulving 2005) further claimed to be part of a uniquely human faculty of "mental time travel," the ability to mentally project oneself into the future as well as into the past (W. Roberts 2002; Suddendorf and Corballis 2007, 2008a; Addis, Wong, and Schacter 2007). We return to this idea at the end of the section, but behavior indicative of future planning is discussed primarily in Chapter 11 in the context of control by delayed reinforcers. This section summarizes current approaches to studying animal episodic memory (for further details see Crystal 2009).

Episodic-like memory in scrub jays

The study of episodic memory in animals began with a landmark experiment by Clayton and Dickinson (1998, 1999) showing that Western scrub jays (*Aphelecoma californica*) remember the location, time, and identity of items they store. They referred to the birds' memory as *episodic-like* because it satisfies the original definition of episodic memory (Tulving 1972) as a memory for what, where, and when of a unique experience but (necessarily) without any evidence of autonoetic consciousness. Jays stored peanuts and waxmoth larvae ("waxworms"), a greatly preferred food, in the sand-filled compartments of plastic ice cube trays placed in their home cages. Each tray was surrounded with a unique arrangement of colored Lego bricks to make it spatially distinct. In several pairs of caching episodes the birds cached peanuts in one side of a tray and waxworms in the other, sometimes in one order and sometimes in the other (Figure 7.23). The two episodes were separated by 120 hours with the opportunity to retrieve items from both sides of the tray four hours after the second caching episode, that is, 124 hours after the first.

In a series of such trials the birds learned that when worms had been cached 124 hours ago they had rotted and become distasteful whereas four hours after caching they were still fresh. Peanuts were always fresh. Thus if the birds could remember where they had cached each type of item and how long ago, they should search for worms when worms had been cached more recently and for peanuts otherwise. This is what they began to do within as few as four matched pairs of caching episodes, and they continued to choose appropriately in tests with no items in the trays, when they could not be using odors or other direct cues (Figure 7.23). Control birds for which worms did not rot always searched for worms first, showing that worms were not simply selectively forgotten. A series of studies with variations of this design (see de Kort, Dickinson, and Clayton 2005) showed that the scrub jays' memory for their caches also integrates location, time, and identity information and can be used flexibly, properties which Clayton and colleagues suggest further qualify it as episodic-like. For example (Clayton, Bussey, and Dickinson 2003), the jays' choices change appropriately when they receive new information about the decay rate of an item during the retention interval.

The findings with scrub jays stimulated analogous studies with mammals, partly in the hope of finding a tractable animal model for neurobiological work (see Morris

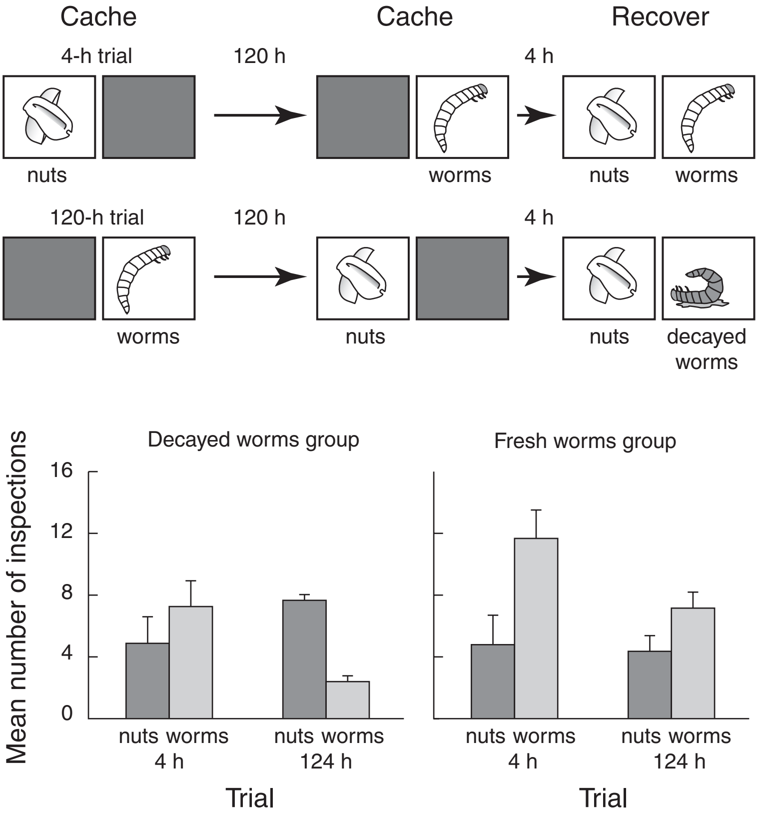


Figure 7.23. Procedure and results for Clayton and Dickinson's (1998) test of episodic memory in scrub jays. Each bird had both types of trials diagrammed at the top; birds in the control group encountered only fresh worms in the recovery phase. Dark squares signify a half of the storing tray unavailable for caching. Lower panels: mean number of inspections directed toward the peanut and worm halves of the tray by birds in the two groups during recovery following both types of trials. After Clayton and Dickinson (1998) with permission.

2001; Eichenbaum et al. 2005; Dere et al. 2006). In the most successful, Babb and Crystal (2006a) demonstrated that rats could remember where in a radial maze a distinctive food (chocolate) had been at a particular time in the past. The first time rats visited the maze on any given trial, a different four of its eight arms were open; three held rat chow and one held chocolate, greatly preferred by the rats. After a retention interval of one or 25 hours, a rat was returned to the maze with all arms open. Rat pellets were in the arms blocked in the first part of the trial; in addition if the retention interval had been 25 hours, chocolate had "replenished," that is, it was back where it had been before. Accordingly, the rats became more likely to visit the chocolate arm within the first four arms visited after the long but not the short retention interval. Once they were performing well, chocolate was degraded by making the rats mildly ill after eating chocolate in their home cages during a 25-hour retention interval. They were much less likely to revisit the chocolate arm on the next test, showing that their memory of the first part of the trial included a representation of a specific food in a specific location (see also Babb and Crystal 2006b; Crystal 2009).

Unexpected questions

Not all agree that the experimental approach pioneered with the scrub jays and adapted for rats is the best or only nonverbal test of episodic memory. One limitation is that the animals are exposed over repeated trials to limited kinds of sequences of events. Correct responding in the tests indisputably requires remembering what was where and how long ago, but the animals' training can be seen as teaching a complex conditional matching to sample task based on trace strength and/or time since the study episode (Zentall et al. 2001; W. Roberts 2002; Eichenbaum et al. 2005; W. Roberts et al. 2008). In contrast, episodic memory in people involves the spontaneous encoding of unique experiences later reported on by answering an unexpected question (Zentall 2005a). Zentall and colleagues (Zentall et al. 2001) cleverly demonstrated that pigeons can "answer an unexpected question" by first training them to "report" whether they had just pecked or not; that is, occurrence or nonoccurrence of pecking was the discriminative stimulus for a color choice. When the opportunity to "report" was introduced into a second context following pecks induced in another way, the birds made the choice previously associated with pecking on about 70% of the first four trials. However, although this study may have captured one aspect of episodic memory, it was memory that had lasted only a few seconds whereas episodic memories in people may be long-term memories (Hampton and Schwartz 2004).

Habituation and episodic-like memory

This drawback is not shared by the test of habituation depicted in Figure 7.3, which can be interpreted (Eacott and Norman 2004) as tapping episodic-like memory in rats. This interpretation depends on the idea that the temporal aspect of human episodic memory is experienced not so much as a specific time ("in July 2003"), but as a context of other experiences ("during my trip to Kenya"). In the situation used by Eacott and Norman (2004; see Figure 7.3), rats' spontaneous exploratory behavior showed that they remembered which side of a chamber and against which colored background (context) a particular object was on up to 30 minutes ago. These findings were obtained after fairly brief exposures; allowing the rats to explore each of the training configurations for longer would likely result in longer-lasting memories. In any case, this paradigm shares two important features with the "unexpected question" paradigm for pigeons. The animals show what they have encoded spontaneously, and because no specific reinforcement is involved they cannot be encoding the experiences in the first phase of trials in preparation for being asked about them later. This and related habituation paradigms have been used effectively in neurobiological studies of episodic like memory in rats and mice (Dere et al. 2006; Crystal 2009).

Remembering versus knowing

In tests of recognition memory in the laboratory, people may be asked whether they remember seeing an item before or merely know it was shown. "Remembering" in this context is identified with episodic recollection whereas "knowing" is simply a sense of familiarity. The everyday counterpart of remembering versus knowing is the difference between a rich recollection of a previous encounter with someone and merely knowing one has seen them somewhere before. When the results of forced choice tests of recognition are represented as ROC curves (Box 7.3), the data can be decomposed into "remember" and "know" components, although this interpretation is somewhat controversial (Yonelinas and Parks 2007). The same pattern can be reproduced in rats' olfactory recognition (Box 7.3; Fortin, Wright, and Eichenbaum 2004). Moreover, consistent with evidence from humans and with the results from serial probe recognition described in Box 7.2, hippocampal lesions selectively affect the "remember" component. What the hippocampus does in rats other than record episodic memories (if that) is at least as controversial as how best to test nonverbally for episodic memory, so this evidence is hardly conclusive. However, because people require an intact hippocampus for episodic memory, dependence on the hippocampus can be seen as one of the necessary if not sufficient properties of episodic-like memory in another mammal (Eichenbaum et al. 2005; Ferbinteanu, Kennedy, and Shapiro 2006). In summary then, the findings described in Boxes 7.2 and 7.3 together with others such as data from Eacott and Norman's (2004) habituation paradigm indicate that rats' memory for recently presented items shares many functional properties with human episodic memory (Hampton and Schwartz 2004; Eichenbaum et al. 2005; Ferbinteanu, Kennedy, and Shapiro 2006; Crystal 2009).

Box 7.2 Olfactory Memory in Rats

Although rats are nocturnal, lack color vision, and have rather poor visual acuity (Prusky and Douglas 2005), traditional studies of rats' discrimination learning (Chapter 6) relied heavily and anthropocentrically on visual cues. But rats are much better able to discriminate among and learn about flavors and odors, and recent studies have capitalized on this ability to study their memory, often with the aim of analyzing its neural basis. A very effective and simple procedure involves allowing the rat to dig in a small sand-filled bowl to find food buried at the bottom. Odors are introduced by mixing common household spices or other substances into the sand. Perhaps partly because they come into direct contact with the odors while digging for food, rats quickly learn to discriminate familiar from novel odors and can discriminate up to 10 or more sequentially presented odors from other familiar odors presented on previous days (see Box 7.3). Visual cues and textures on the bowls are also effective cues in such a digging task (Botly and De Rosa 2007) as are the materials in the bowls (Sauvage et al. 2008).

A continuous non–matching to sample task with odors (Wood, Dudchenko, and Eichenbaum 1999) consists of letting rats encounter one sand-filled cup at a time, each in a different random location in an open field. If its odor differs from the odor of the last cup presented, it holds food and the rat digs; if the odor is the same, there is no food and rats learn to withhold digging and turn away. Then another cup is presented, and the same rule holds, and so on. (Note that various controls, such as unbaited probe trials, are always included in such studies to show that the rats are not smelling the food in baited bowls.) In a more elaborate variant of this task diagrammed in Figure B7.2, a series of five odors, A–E, is presented, a different selection from 20 familiar odors on each trial (Fortin, Agster, and Eichenbaum 2002). Memory for items in the sequence can be tested in a serial probe recognition procedure in which the rat is given a choice between an odor from the current sequence (unrewarded) and an odor not in the sequence (rewarded). As shown in Figure B7.2, recognition is excellent, with a clear recency effect, that is, better performance for items at the end of the sequence.

Memory for relative position in the sequence can also be tested by presenting two odors from the sequence and rewarding choice of the earlier one. Rats display excellent memory for sequential order in this test. Not surprisingly, performance is better with odors farther apart in the sequence. Rats trained in the sequence memory task and then given hippocampal lesions showed normal recognition memory but their discrimination of relative position was severely impaired (Figure B7.2). Thus the lesioned rats had nearly normal memory traces in that they could discriminate odors in the present list from those in earlier lists about as well as intact rats, yet their near-chance performance in the sequential order task suggests that this task calls upon a different mechanism than comparing trace strengths (see also Kesner, Gilbert, and

Barua 2002). One possibility discussed in Section 7.6.3 is that the list is encoded as a series of events much like an episode. Whether this analogy is accepted or not, the way in which lesions dissociate simple recognition from memory for sequential order is a nice example of how the results of neurobiological research can inform theory at the level of "black box" mechanisms.

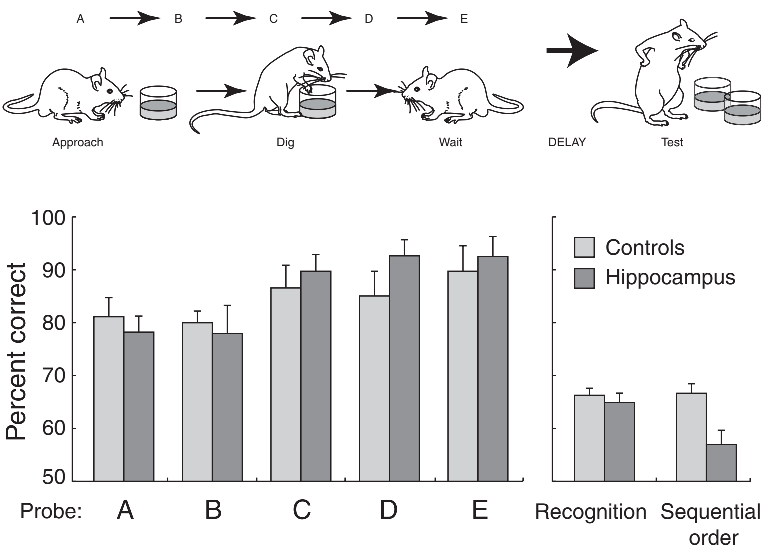


Figure B7.2. Procedure and data from tests of rats' memory for sequences of odors. In the exposure phase, the rat encounters five odors, A–E, 2.5 minutes apart. In the test (top right), recognition is tested by offering one odor from the list and one not in the most recent list; choice of the latter is rewarded. Memory for sequential order is tested by offering two odors from the list and rewarding choice of the one presented first. From Fortin, Agster, and Eichenbaum (2002) with permission.

Box 7.3 Familiarity, Recollection, and Signal Detection

Just as in tests of perception, in tests of memory the behavior taken as evidence of an underlying cognitive process can occur for other reasons. The pigeon in a delayed matching experiment might prefer to peck a red key rather than a green one regardless of which was the sample, or a rat might prefer to visit some arms of a radial maze rather than others. Signal detection analysis (Chapter 3) again provides a way to distinguish such response biases from effects on memory. In studies of human recognition memory, ROC curves can be generated when subjects study a list of words and are tested by presenting words from the list along with an equal number of words not in the list. Subjects classify each word as "new" or "old." Saying "old" to words in the list is a hit; "old" for a new word is a false alarm, as if subject is making a discrimination among memory traces that overlap in strength much as perceptual effects do (see Figure 7.22).

Data along a given ROC curve may be collected either by varying subjects' criteria (e.g., "say 'old' only if you're very sure") or by collecting confidence ratings along with "new" versus "old" responses. Figure B7.3 shows an example. Unlike the ROC curves in Chapter 3, it is asymmetrical. With a high criterion, saying "old" only when they are very sure, nearly all subjects' "old" responses are correct and very few are false alarms. This asymmetry has been interpreted as meaning that performance is the sum of two separate processes: recollection or episodically remembering the item, which is an all-or-none or threshold process, and familiarity or "knowing," which by itself describes a symmetrical ROC curve (Yonelinas and Parks 2007). In normal adults, different instructions may dissociate these processes; in amnesic patients, only the second process may be evident.

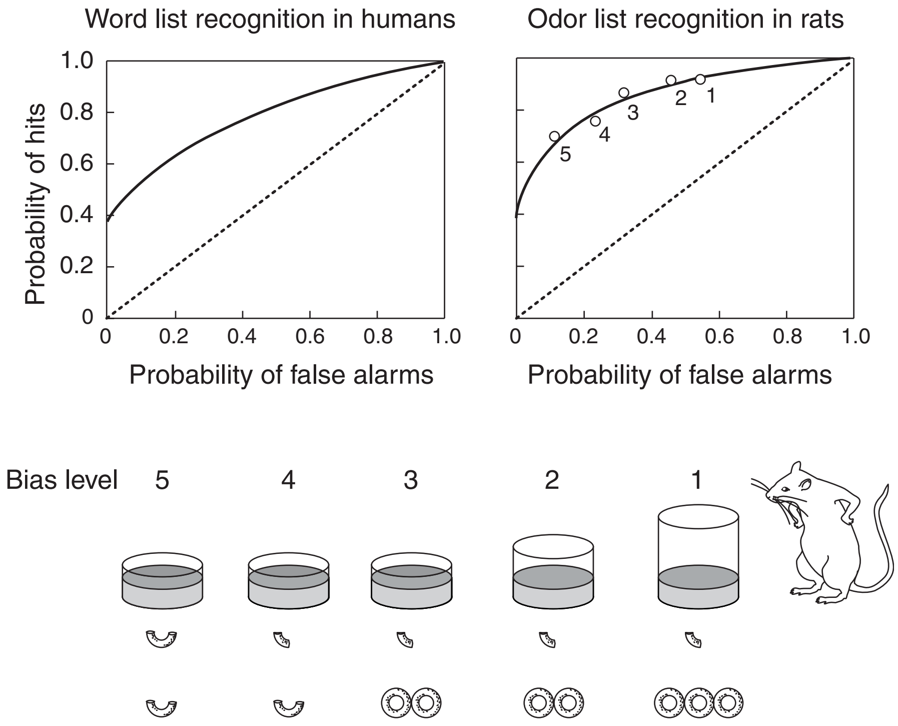


Figure B7.3. Typical ROC curve from tests of word recognition in which people rate test words as "old" (i.e., in the studied list) or "new" and data from rats in a test of odor recognition. Rats are reinforced for digging in a test cup with an odor not in the list and digging in a standard alternative cup for "old" odors. For the five bias levels, the rats' criterion was varied as indicated in the diagram. For example, at bias level 1, a high level of false alarms (choosing "old") results from a relatively large reward (three whole cereal pieces) for digging in the neutral cup versus a small reward in a tall test cup, difficult to dig in. Adapted from Fortin, Wright, and Eichenbaum (2004) with permission.

In a forced choice test of odor recognition using a procedure similar to that diagrammed in Figure B7.2, rats encountered ten odors in succession and were tested 30 minutes later with these and ten other odors (Fortin, Wright, and Eichenbaum 2004). They were rewarded for digging in test cups with new odors and for digging in an alternative, neutral, cup when an "old" odor was present in the test cup. The criterion was varied by varying both the height of the test cup and the amount of reward for choosing the "old odor" cup as diagrammed in Figure B7.3. Intact rats' recognition data (Figure B7.3) described an asymmetrical ROC curve much like normal humans.' As discussed in the main text, these findings can be taken to support claims that rats have episodic-like memory.

Signal detection theory has been applied to many other issues in the study of animal as well as human memory (Marston 1996). Examples include the work of Wixted (1993) on pigeons' delayed matching with samples of food and no food and Blough's (1996) analysis of the sources of errors in delayed matching tasks. Shettleworth and Krebs (1982) used ROC curves to show that both caching site preferences and memory contribute to marsh tits' retrieval of stored seeds in the laboratory.

Conclusions: Elements of episodic memory?

All the experimental approaches sketched in this section involve testing memory for the "what, where, and when" of some unique recent event. Some paradigms go beyond demonstrating that animals pass a single test to documenting further functional similarities between the animals' behavior and human reports of episodic memory. The variety of approaches that has developed might be taken as welcome evidence of a search for convergent data, but they also reflect the fact that no one approach to date has captured all aspects of human episodic memory in another species. This diversity is consistent with the broad use of the term among students of human memory. For instance, Tulving (e.g., 2005) describes episodic memory in terms of vividly recollected personal experiences, but studies of comparatively short-term memory for lists of items in the laboratory (e.g., Kohler, Moscovitch, and Melo 2001) are also described as testing episodic memory. Accordingly, both the original Clayton and Dickinson paradigm, with memories lasting hours or days, and studies with rats remembering odors or locations of objects for a few minutes are legitimate candidates for animal analogues. Arguably (Crystal 2009) the disparate tests for episodic-like memory each tap one or more of its elements. Other elements include whether the features of an episode are integrated in memory or treated as separate items of information (Skov-Rackette, Miller, and Shettleworth 2006) and whether the temporal component, if any, is time of day, time in the past, or something else (Roberts. et al. 2008).

We will see elsewhere that breaking some global ability such as counting (Chapter 10), theory of mind (Chapter 12), or communication (Chapter 14) into components and asking which are shared among which species, to what degree, and why (in functional and mechanistic senses) can be a more productive approach to comparative research than asking all-or-nothing questions about whether animals have the ability in question or not. The study of animal episodic-like memory has progressed in this way. It leads to the provisional conclusion that a variety of species, even some invertebrates (Pahl. et al. 2007), share with humans a propensity to encode the "what, where, and when" of unique events and that some of these memories share other functional properties of human episodic memory. It is possible, however, that by eschewing speculation about subjective experience, researchers testing animals are missing the essence of episodic memory, which is that by allowing people to mentally reexperience events it supports "time travel" not only into the past, but into the future, to imagine and plan for entirely new kinds of events in a way that is impossible on the basis of learned responses to old events (Suddendorf and Corballis 2008a). Indeed, episodic memory has most likely evolved so people can imagine and plan for the future, not so they can relive the past. On this view (Suddendorf and Corballis 2008a), the functional similarities between nonhuman and human memory reviewed in this section fail to capture a key—and uniquely human—feature of episodic memory. We revisit this discussion in Chapter 11.

7.7 Summary and conclusions

Memory is the most general term for the process that allows animals to base their behavior on information from individual past experience. The questions we can ask about memory therefore parallel those asked about learning in Chapters 4 and 5: what are the conditions under which memories are acquired, the contents of memory, and the effects of memory on behavior? Accordingly, many of the conditions affecting memory parallel those affecting learning. These include frequency, duration, and number of exposures to the to-be-remembered events, proactive and retroactive interference from previous, similar experiences, and the similarity between the current context and that in which the memory was acquired. Most such conditions are thought to be important regardless of what is to be remembered, suggesting that even if it is possible to identify different memory systems in some sense (Sherry and Schacter 1987) they will have a number of common properties. Much contemporary research on animal memory is devoted to analyzing its neural and genetic basis, often using simple paradigms introduced in this and earlier chapters.

Since before the beginning of experimental studies of animal cognition, people have wondered whether some animals have better memories than others. Section 7.4 examined several research programs inspired by this question, including early comparative studies of delayed response, recent ecologically based comparisons of closely related species that rely on spatial memory to differing extents in the wild, and comparisons of serial position effects in pigeons, monkeys, rats, and people. Any attempt to collect meaningful comparative data on memory faces a number of challenging problems such as to how to deal with possible contextual variables. The research reviewed here has revealed at most quantitative differences among species in capacity and durability of memory.

Finally, Section 7.6 introduces attempts to devise nonverbal tests for processes that are accompanied by distinctive subjective states in humans, here metacognition and episodic memory. In a number of situations animals show behavior consistent with metacognition, but nearly all the data to date can be explained in terms of sensitivity to publicly observable cues rather than to private states. Research on episodic memory has largely focused on tests that capture one or more of its key elements, especially formation of an integrated memory for the "what, where, and when" of a unique experience, referred to as episodic-like memory. A variety of species, in a variety of situations, show at least elements of episodic memory. The important notion of functional similarity, or focusing on what cognitive processes allow animals to do rather than on the subjective states that accompany them, is illustrated very well with research on metamemory and episodic-like memory. It will also come in handy in future chapters.

Further reading

The development of contemporary research on animal memory and other aspects of cognition can be traced in a series of edited books. Medin, Roberts, and Davis (1976); Hulse, Fowler, and Honig (1978); and Roitblat, Bever, and Terrace (1984) are among the landmarks. Chapters in Wasserman and Zentall (2006b) review more recent work. *The Science of Memory: Concepts* (Roediger, Dudai, and Fitzpatrick 2007) contains brief discussions of all aspects of memory by major researchers in the field. Eichenbaum's (2008) text is a good introduction to neurobiological mechanisms of memory in all species. Bouton and Moody (2004) discuss the interface between conditioning and memory, Balda and Kamil (2006) comprehensively review the research on food-storing corvids, and Wright (2006) does the same for serial order memory. For discussion of metacognition, see the book edited by Terrace and Metcalfe (2005) and the "forum" of pieces by many of the major players in the 2009 edition of the online *Comparative Cognition and Behavior Reviews*.

Part II

Physical Cognition

Each of the next three chapters discusses how animals acquire and use information about a specific aspect of the physical world: space (Chapter 8), time (Chapter 9), and number (Chapter 10). Spatial, temporal, and numerical cognition each involve some domain-general processes as well. For instance, Weber's Law appears in each of Chapters 8–10 as do basic principles of learning, memory, and discrimination. But understanding navigation, timing, and counting also requires some domain specific theoretical concepts and perhaps cognitive mechanisms. Effective spatial behavior inherently involves acquiring and using vector-like information, that is, information about distances and directions. Historically, debate has revolved around suggestions that such information is stored in a maplike representation. This debate continues, as we will see. More recently there have also been suggestions that multiple kinds of spatial information are combined in ways not captured by current models of associative learning. Similarly, analyzing how animals respond to the universal cycle of day and night requires particular concepts such as pacemakers and entraining agents and models of its own which may or may not be applicable to timing events at shorter intervals. And the study of numerical cognition is a burgeoning model for comparative research in the way it integrates complementary experiments with human adults, children, and diverse nonverbal species. The over simple anthropocentric question, "Can animals count?" is now replaced by a clear evolutionary framework in which numerical cognition is seen as consisting of several subprocesses that may be shared among species to different extents.

As its title indicates, Chapter 11, "Cognition and the consequences of behavior: Foraging, planning, instrumental learning, and using tools," differs from the other chapters in this section in discussing a seemingly diverse set of topics. But for each of them the key issue is understanding how a specific kind of activity is influenced by its outcome. In the section on foraging we see how functional models, primarily the predictions of optimal foraging theory, have been brought together with data and theory about the control of instrumental behavior. Then we look more deeply at the kind of learning and representation underlying behavior that is acquired and maintained because of its consequences, along the way returning to and enlarging upon the discussion of associative learning theory in Chapter 4. Finally in the sections on planning and tool use we look at two kinds of behavior traditionally thought to be uniquely human but increasingly found in other species and ask whether they depend on any special processes. Do tool-using apes and birds, for example, understand how tools work?

8

Getting Around: Spatial Cognition

Limpets are small mollusks that live on coastal rocks where they are exposed to the air at low tide. As it grows, each limpet erodes a scar on the rock that matches the irregular outline of its shell. By clinging tightly to this spot during low tide, the limpet can protect itself from dehydration (and from predators, as anyone who has tried to pry one loose can testify), but to find food it must forage over the rock while the water is high (Cook et al. 1969).

Many mobile animals face the same problem as the limpet: food and other resources are separated from places of refuge, and the animal has to be able to travel between them without getting lost. There is a premium on making this trip efficiently rather than wandering at random until the goal is found, which in the limpet's case might be too late to prevent drying out. The limpet's problem is a miniature one in space and time compared to the orientation problems solved by other species (Figure 8.1), but they all have certain features in common. Each individual or group of individuals is locating its own home, hoards, or other resources. Therefore, they need some sort of acquired representation of the goal's location or how to get to it. Some animals, like the limpet, create such a representation in the external world in the form of a chemical trail (Chelazzi 1992). Under some circumstances, animals can find their way by directly approaching cues emanating from their goals or learning sequences of responses. However, we will be most concerned with how animals acquire and use information that is inherently spatial, that is, information about distances and directions. Mathematically, this is vector or shape information. And although long-distance navigation may involve amazing feats of perception, learning, and memory (see Box 8.1), we will be almost entirely concerned with travels of a meter or less to at most a few kilometers.

Because acquiring and acting on spatial information appears to have different computational requirements from learning to predict temporal sequences of events, we might expect to find adaptively specialized, domain-specific mechanisms of spatial learning and/or performance, different from those for associative learning (F. Dyer 1998; Gallistel 2003).This issue can be addressed in terms of the three fundamental questions about learning from Chapter 4—the conditions for learning, the contents of learning, and its effects on behavior. Spatial performance rules can be thought of as servomechanisms. That is, they generate behavior that reduces the discrepancy between the animal's current position and a remembered target position (Cheng 2000). Although mechanisms for

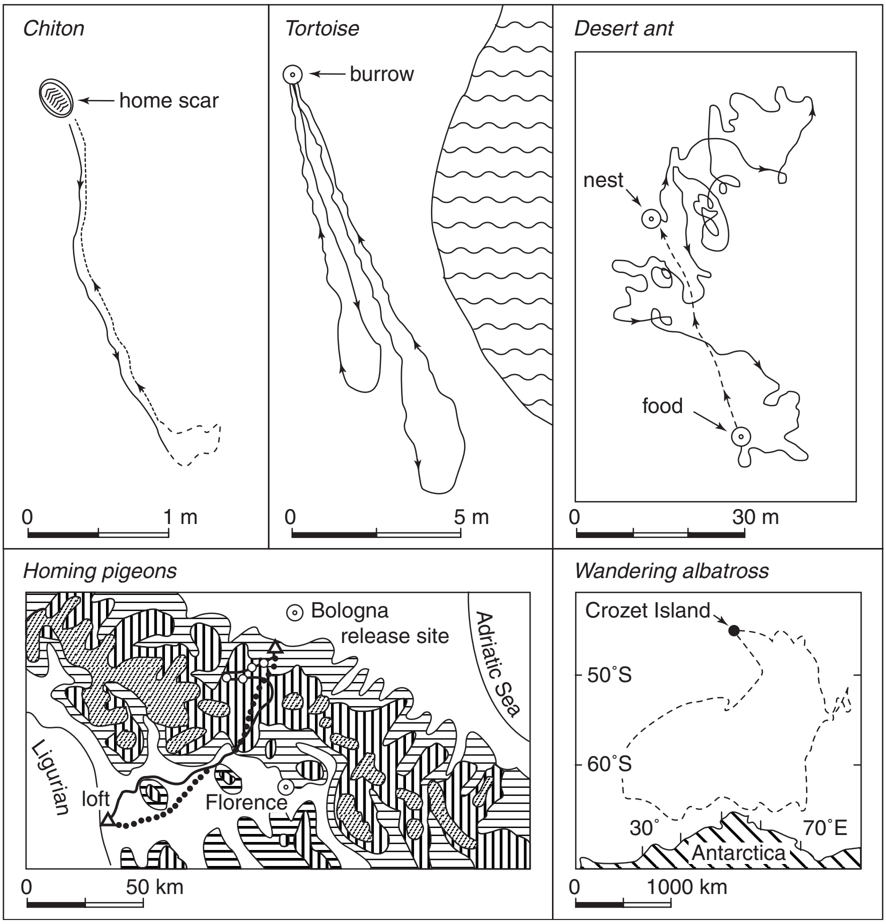


Figure 8.1. Homing paths of individuals from five species, illustrating the wide range of spatial scales over which journeys out from a central place and back may take place. After Papi (1992b). Tortoise from Chelazzi and Francisci (1979); albatross from Jouventin and Weimerskirch (1990). Redrawn with permission.

Box 8.1 Long-Distance Migration

The astonishing ability of animals from all taxa to find their ways over hundreds or thousands of kilometers is a subject in itself (see Alerstam 2006; Holland, Wikelski, and Wilcove 2006). It has been given a huge boost in recent years by sophisticated satellite tracking systems for recording not only the position but the activities, temperatures, and so forth, of migrating animals. The sensory and neural mechanisms required can also be studied in some of the same species (Frost and Mouritsen 2006). Notwithstanding their vastly different scales, however, long-distance and short-distance travels are largely analyzed with the same basic conceptual framework (Bingman and Cheng 2005). Distance, direction, and position information are important however far one is going, and the degree to which it is maplike is an issue whatever its scale.

Probably the longest-standing subjects in studies of the mechanisms for long-distance migration are birds. Among the many species of small birds that migrate at night, even captive hand-reared individuals exhibit nocturnal activity, so-called migratory restlessness, at the time of year when they would normally migrate (see Gwinner 1996). In indoor cages at night they tend to hop toward the compass direction in which their conspecifics are flying at that time of year. Manipulating the early experience of such birds has revealed a kind of interaction between predisposition and experience that might be called *calibration.* Calibrating a physical measuring instrument means comparing its readings to those of an independent standard and adjusting it so its readings match the standard's. An electronic thermometer might be calibrated against a mercury thermometer, for example. Analogously, one orientation mechanism may be changed by experience so that its outputs more closely match those of a second, independent, mechanism. The primary examples involve calibrating celestial cues against magnetic information.

For example, the primary directional cues for nocturnal migrants are the Earth's magnetic field and, on clear nights, the stars, but the pattern of stars varies with geographic location, time of night, and season, and it changes over geologic time. Insight into how birds nevertheless use the stars to tell direction comes from classic experiments by Emlen (1970) with indigo buntings (*Passerina cyanea*). He raised three groups of birds indoors out of sight of the sky, but late in their first summer two of those groups were exposed to the "night sky" in a planetarium. For one, the stars rotated normally, around the North star, whereas for the other the center of rotation was the bright star Betelgeuse. When all the birds then spent autumn nights in the planetarium under stationary star patterns typical for the time of year, the birds with no experience of the sky were not well oriented, but those exposed to the normal sky oriented Southward, indicating that they had somehow learned to use the stationary star patterns during earlier exposure to the normal night sky. The third group treated Betelgeuse as the North star, flying "south" with respect to it, indicating that the star or star pattern near the center of rotation of the night sky is used to give direction. Magnetic information interacts with this information during normal development (see Able and Bingman 1987; Able and Able 1990; Weindler, Wiltschko, and Wiltschko 1996).

Some species change direction in midjourney, following routes that take them around inhospitable places like the Alps and the Sahara. Young birds raised in captivity show evidence of population-specific genetic programs that specify the duration of migratory restlessness and its direction with respect to the magnetic field (Helbig 1994, 1996). Figure B8.1 shows an example in which two European populations of a single species, the blackcap (*Sylvia atricapilla*), migrate in different directions, and one changes course part way while the other does not. Such inborn tendencies to head in a certain compass direction at a certain season are likely important for the many species in which animals migrating for the first time are not accompanied by experienced adults. This likely includes sea turtles and at least one insect, the Monarch butterfly (Holland, Wikelski, and Wilcove 2006). At the same time, the success of programs for reintroducing migratory bird species to their ancestral flyways by training them to follow ultralight aircraft (www.operationmigration.org) indicates that some species learn details of their migratory routes.

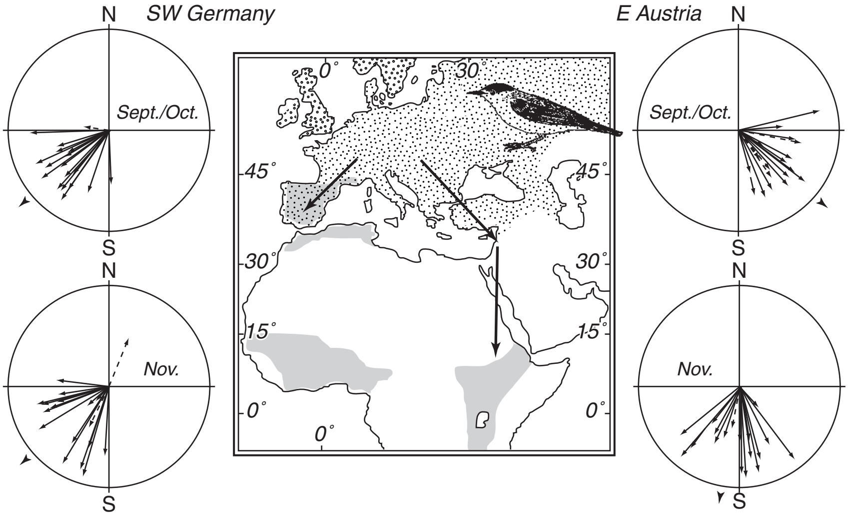


Figure B8.1. Breeding (dotted) and wintering areas (grey) of two populations of European blackcaps with their major migration routes. Arrows inside the circles represent orientation of hand raised birds from the two populations tested in funnel cages early and late during the period when they would normally be migrating. Each vector is the mean orientation of a single bird; the longer the arrow the stronger the directional tendency. Redrawn from Helbig (1994) with permission.

reading out where to go from information about where one is are far from simple (Biegler 2006), the effects of spatial learning on behavior are generally taken for granted: the animal reaches the goal in the presence of the appropriate cues. Much more attention has been devoted to the content of spatial learning. In practical terms, this means discovering what features of the goal control behavior. The most controversial question about the content of spatial learning is "Do animals have cognitive maps?" That is, is spatial orientation in complex environments controlled by an overall representation of distances and directions that allows the animal to select an efficient route when displaced to a new location? This question turns out to be difficult to answer, for two reasons. First, although a map is a powerful metaphor for spatial knowledge, different investigators may mean different things by *cognitive map*. Second, before we can consider whether any animal might have a cognitive map in any sense, we need to consider all the simpler mechanisms animals can use to find their ways to goals (Section 8.1). and how they may be combined (Section 8.2). Section 8.3 discusses how animals acquire spatial knowledge, especially whether any processes different from associative learning are involved. Then, in Section 8.4, we will assess the evidence for cognitive maps.

8.1 Mechanisms for spatial orientation

8.1.1 Dead reckoning

A foraging desert ant (*Cataglyphis fortis*) wanders here and there, taking a long and tortuous path in its search for food, but as soon as it finds a prey item it heads straight back to its nest over a hundred meters away (see Figure 8.1). These ants return to the vicinity of the nest using *dead reckoning,* an internal sense of the direction and distance of the nest from their current position. That they know both distance and direction can be shown by catching an ant in a matchbox just before it starts its homeward journey and releasing it several hundred meters away. It does not head for the nest but takes a path parallel to that which it would have taken from the point of capture. For instance, if the nest was originally to its south, the ant still heads south even if the nest is now to the east (Wehner 1992, 2003). Moreover, when it has gone about the right distance, the ant begins to circle around as if looking for the nest in the place where it should be (Figure 8.2). This behavior shows that the ant must be performing *path integration* on the outward journey. That is, it behaves as if continuously integrating (in the mathematical sense) information about its changes in distance and direction to compute the vector that links it to the nest.

In fact, ants use an approximation in which each direction taken, as perceived by its solar compass (Box 8.2) is weighted by the distance for which it is maintained (Muller and Wehner 1988). The orientation of the straight path reveals the ant's representation of the homeward direction, and the point at which it begins to circle around reveals its representation of the distance from start to nest. Once the ant arrives near where the nest should be, it continues to perform the same implicit computations. Although taking a roughly spiral path, it continually returns to the point where it began searching, as if keeping track of its position with respect to the most likely nest position. This localized search seems to be programmed to overcome the inherent errors of path integration in that the further an ant has traveled from the nest, the wider its spiraling loops when it returns to the nest's vicinity (Wehner and Srinivasan 1981; Merkle, Knaden, and Wehner 2006). This behavior increases the chances that the nest is found, which is vital because the hot sand surface can be lethal to ants that do not escape underground quickly enough.

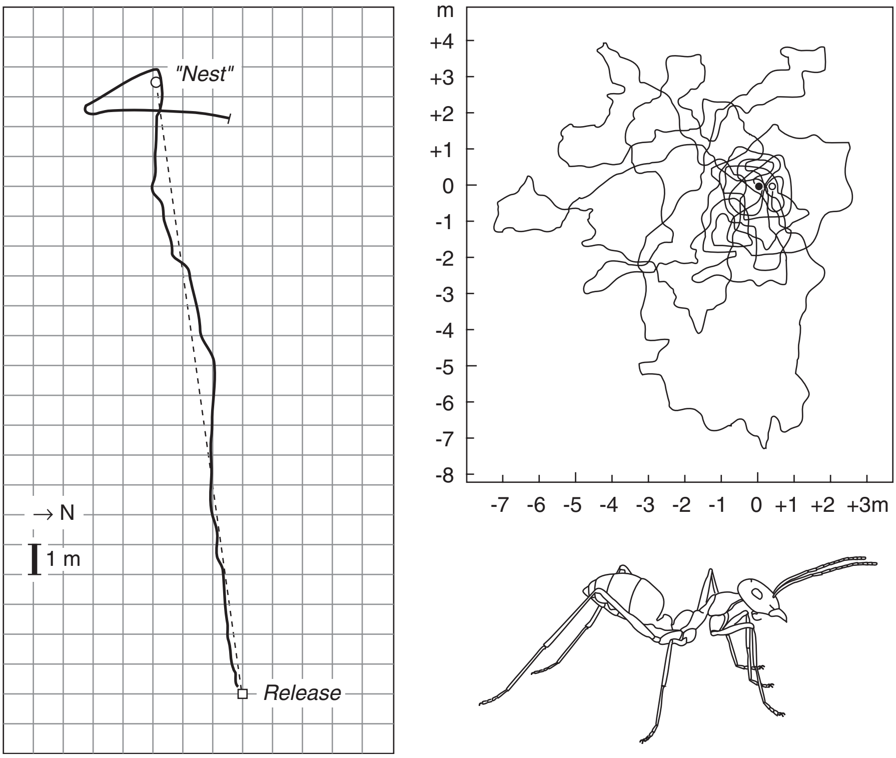


Figure 8.2. Homing in desert ants (*Cataglyphis albicans*). Left: Path of an individual that has just found food and is displaced to unknown territory. The open circle shows where the nest would have been relative to the release site if the ant had been in its home territory. Right: The spiraling path taken by the ant once it arrives near where the nest should be, recorded over one hour. Data redrawn from Wehner and Srinivasan (1981) with permission; ant from Wehner (1992) with permission.

Box 8.2 The Sun Compass

The sun is useless as a landmark because it moves continuously relative to the Earth, but many diurnal animals use it for directional information, that is, they have a *sun compass*. For example, the desert ants in Section 8.1.1 use both the sun and patterns of polarized light it creates in the sky for directional information when computing their paths home from food (Wehner and Müller 2006). If an ant is trained to a food source on a featureless patch of desert at one time of day and then kept in the dark for a few hours, it heads roughly homeward when released even though its direction relative to the sun's position is different from what it was during training. That they are still relying on the sun rather than some subtle landmarks is shown by the fact that ants prevented from seeing the sun in this experiment head off in random directions (Wehner and Lanfranconi 1981).

Reading direction from the sun regardless of the time of day requires both a stored representation of how the sun moves across the sky at the current location and season (an *ephemeris function*) and an internal circadian clock (Chapter 9). The sun's position overhead is converted to a compass direction (i.e., direction relative to North) by computing the sun's *azimuth*. This means taking the imaginary arc connecting the sun with the closest point on the horizon and measuring the angle on the surface of the earth between that point and North (Figure B8.2a). This kind of computation is implied by statements like "The sun is in the South" at noon in the Northern hemisphere. But although the sun *is* in the South at noon, because the sun's elevation at a given time of day changes with the time of year, the sun's azimuth changes at different rates at different times of year and at different times of day (Figure B8.2a). Thus to use the sun for directional information, animals must acquire some

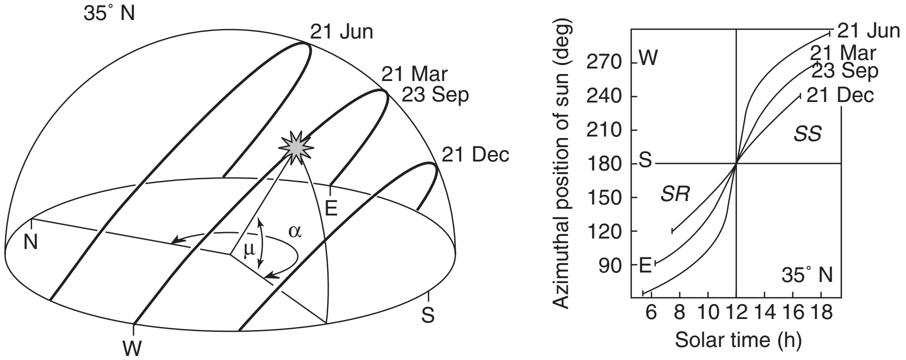
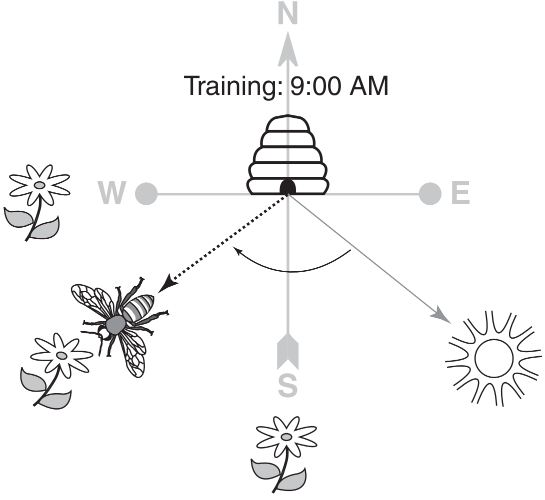


Figure B8.2a. How the apparent path of the sun across the sky (arcs) varies with time of year at a particular latitude, 35° North. Angle α on the surface of the earth is the sun's azimuth; μ is the sun's elevation. Ephemeris functions (right) give the sun's azimuth as a function of time of day and time of year. After Wehner (1992) with permission.

representation of the local ephemeris function and continually update it. This process has been studied in honeybees by restricting the experience of newly hatched foragers when they first leave the hive (F. Dyer and Dickinson 1994). The results indicate that, in a kind of process general to many kinds of learning, bees begin life with a crude default ephemeris function, a best guess about the conditions they are likely to meet, and experience fine-tunes it (F. Dyer and Dickinson 1996).

To show definitively that an animal is using a sun compass it is necessary to shift its internal clock and test whether orientation shifts accordingly. (As discussed in Chapter 9, shifting the clock means keeping the animal under an altered day-night light cycle for several days.) The logic of clock shift experiments is depicted in Figure B8.2b with a hypothetical example using bees. Homing pigeons have also been tested extensively in such experiments (Papi and Wallraff 1992). Of course in laboratory studies of small-scale spatial learning, animals cannot use a sun compass because the

Figure B8.2b. The logic of clock shift experiments, showing how to tell which way a clock-shifted animal will head. In this example, a bee trained to find food in the position indicated has its clock shifted back 3 hours by turning the lights on 3 hours later in the morning. At 9 AM it experiences the time as 6 AM. When it flies from the hive it will maintain the same angle to the sun as when heading to the goal at 6 am before clock shifting.



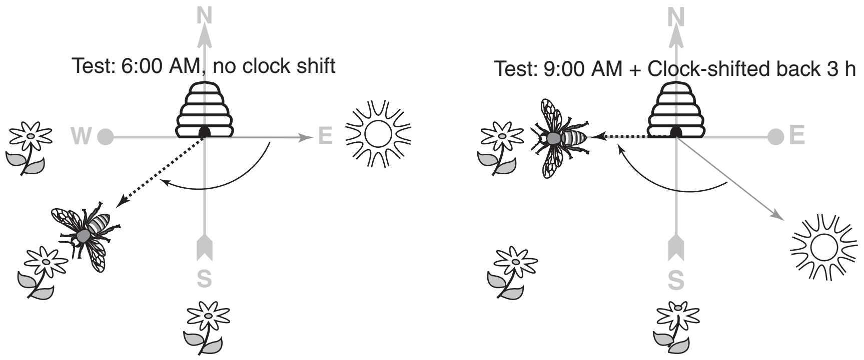


Figure B8.2b. (Continued)

sun is not visible. However, some birds have proved to use the sun compass in learning simple spatial discriminations outdoors under sunny skies. These include homing pigeons (Bingman and Jones 1994; Chappell and Guilford 1995), scrub jays (W. Wiltschko and Balda 1989), and black-capped chickadees (Sherry and Duff 1996). For example, when scrub jays were clock-shifted by 6 hours between storing and retrieving seeds in an outdoor arena, the birds relied on their sun compass in spite of the fact that distant landmarks were visible outside the arena. However, the relative importance of the sun compass vs. other spatial information will vary with species and circumstances as suggested by the discussion of pigeons' homing in the main text.

Dead reckoning is one of the most basic and ubiquitous ways in which animals keep track of their location with respect to a known position. (*Dead reckoning* is a navigators' term; it is generally used interchangeably with *path integration.*) It has been studied most in insects such as ants, bees, and spiders (Wehner and Srinivasan 2003). Indeed, although possible examples of dead reckoning in humans were noted by Darwin (1873), its role in spatial learning by rats and other small mammals was almost completely overlooked before Mittelstaedt and Mittelstaedt (1980) described it in gerbils (*Meriones unguiculatus*). In the situation they studied, mother gerbils and their pups had a nest at the edge of a large circular arena. If the pups were taken from the nest and placed in a cup somewhere in the arena, the mother soon began to search for them. When she found the pups, she picked one up in her mouth and ran almost straight back to the nest, even in total darkness and even if her outward path had zigzags and detours. If the nest was moved by rotating the edge of the arena while the mother was at the stationary cup, she returned to the starting point of her journey like the desert ant, ignoring any cues emanating from the nest in its new location. In contrast, if the cup was rotated briskly while the mother gerbil was in it, she compensated for the rotation and headed straight back to the nest as before. But if the cup was rotated slowly or slowly moved sideways, the gerbil did not compensate and was misoriented. The effect of rotation speed reflects that fact that in mammals information about changes in angular orientation is processed by the vestibular system, which senses accelerations and decelerations above a certain threshold (McNaughton, Knierim, and Wilson 1995; Wallace et al. 2002).

More extensive studies like these have been done by Etienne and her colleagues with golden hamsters (*Mesocricetus auratus*) hoarding food from the center of an arena back to their nest and increasingly with rats (Etienne and Jeffery 2004). Geese carried in a cart up to a kilometer or so from their home also appear to home by dead reckoning (Saint Paul 1982). They obtain information about displacement from the patterns of visual flow. If they cannot see out of the cart for parts of the outward journey, they act as if discounting this part of the trip. This intriguing little study has apparently never been followed up, and few further observations relevant to path integration in birds have been reported. Pigeons show little evidence of relying on visual flow for position information in a laboratory task (Sutton and Shettleworth 2005). In contrast, a great deal is known about how ants and bees compute distances and directions of travel from visual and other cues (Boxes 8.2 and 8.3). Reliance on nonvisual, vestibular, cues for direction is especially appropriate for nocturnal species like hamsters and rats. However, although the sensory inputs are very different in mammals and insects, the implicit computations on them are similar. For example, when forced to take an outward journey consisting of two segments connected at a given angle, ants, spiders, bees, and several species of mammals make similar angular errors when heading home (Etienne and Jeffery 2004).

Box 8.3. Odometers of Honeybees and Desert Ants

We see in the main text that honeybees and desert ants behave as if having an *odometer,* a mechanism for measuring distance traveled. But bees generally fly whereas ants walk, and the odometers of the two species use correspondingly different information. For flying honeybees, distance is measured by *optic flow,* the angular motion of images past the eyes. Evidence comes from experiments such as the one diagrammed in Figure B8.3a, in which bees flew down a tunnel decorated with vertical black and white stripes to find sugar water (Srinivasan et al. 1996). With the food at a fixed location, bees learn where to expect it as evidenced by their circling around over the usual place of food in unrewarded tests. When image motion was eliminated by replacing the vertical stripes by horizontal ones for the tests, the bees searched equally at all distances. When the tunnel was wider or narrower than usual, the bees searched at a greater or lesser distances respectively (Figure B8.3a). To understand why the effect of the tunnel's width, that is, the distance of images from the eyes, means that angular image motion is important, think of how nearby objects cross your visual field faster than those farther away when you are in a moving car. Changing the density of the pattern inside the tunnel also changes the rate of image motion, and accordingly, in natural landscapes the bees' subjective estimates of distance as revealed in their dances (Section 14.2.1) is greater when they have flown over a richly patterned landscape than when they have flown the same distance over water (Tautz et al. 2004).

Desert ants walk across rather featureless terrain. Accordingly they estimate distance using about the only cue available, the number of steps they have taken. In the most direct demonstration that the ant's odometer is in fact a pedometer, ants that had walked along a straight channel from the nest to food were captured before starting home and fitted with stilts made of pig bristle or made to walk on stumps by painlessly removing the last segment of their legs (Wittlinger, Wehner, and Wolf 2007). Then they were released in a long parallel test channel and—as in the tests with bees—the point at which they began circling around searching for the nest was recorded. The altered ants walked in a remarkably normal way. As a result those with stilts went too far, and those with stumps not far enough (Test 1 in Figure B8.3b). In contrast, ants that had stilts or stumps throughout a whole round trip estimated the nest location accurately (Test 2 in Figure B8.3b).

Normally ants compute a straight homeward path by path integration over a winding outward journey as in Figure 8.2. What if part of the journey is over hilly terrain? Remarkably, the ant's pedometer compensates for hills, perhaps relying on gravity sensors in the joints (Grah, Wehner, and Ronacher 2005). Ants that either left the nest over a hilly channel and were transferred to a flat

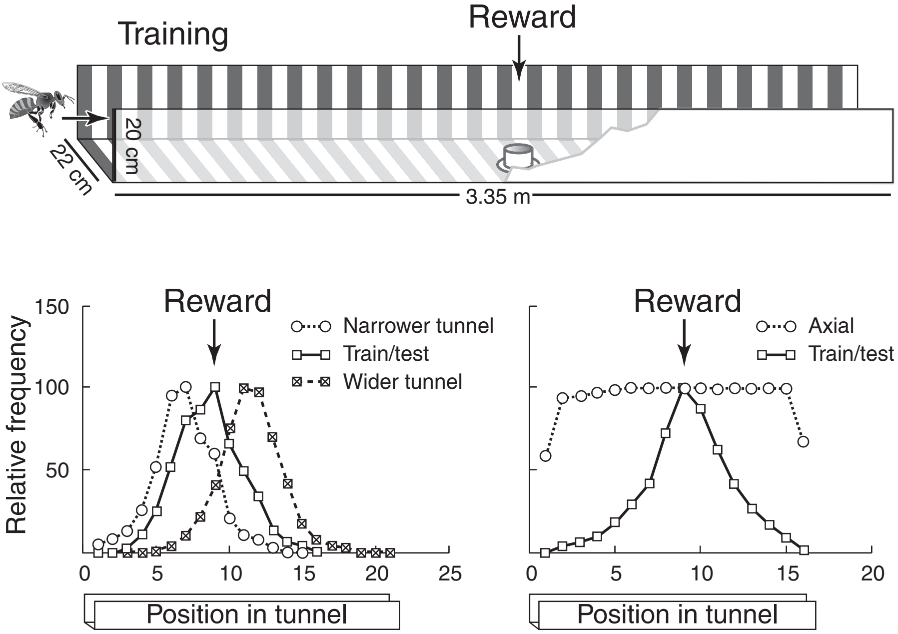


Figure B8.3a. Setup and results of experiment testing influence of visual flow on distance estimation in honeybees. The data are proportions of searches, normalized to 100 at the peak place of searching. The measure of position in the tunnel is number of vertical stripes. All bees were trained to the same position, the one used for trials marked "train/test" but then tested with wider and narrower tunnels or axial stripes in the same tunnel (right panel). Adapted from Srinivasan et al. (1996) with permission.

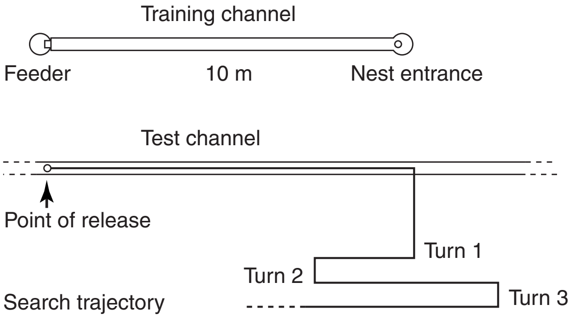


Figure B8.3b. Data from test of odometry in ants on stilts and stumps that was otherwise analogous to the study with bees in B8.3a. Adapted from Wittlinger, Wehner, and Wolf (2006) with permission.

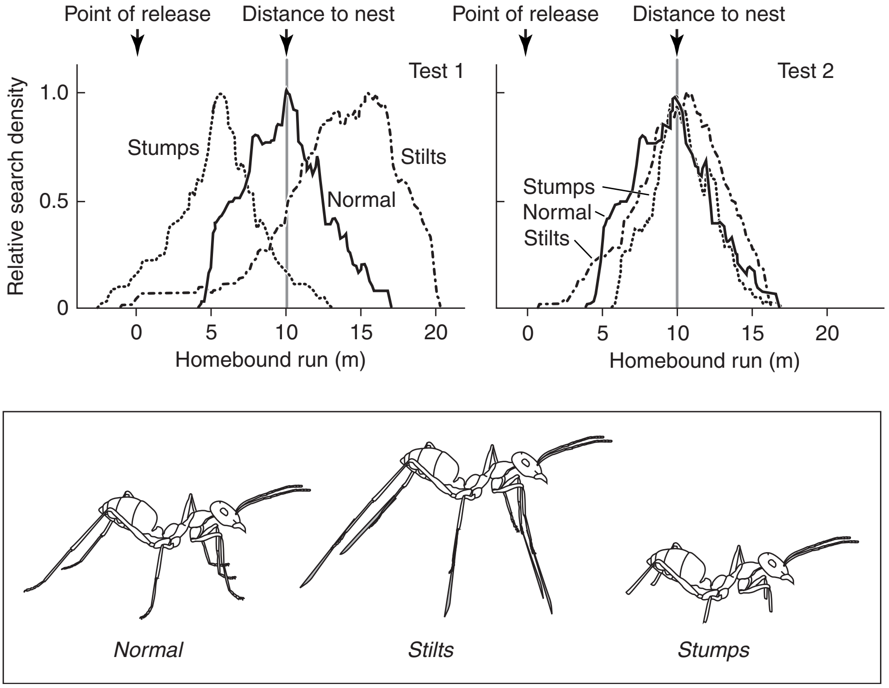


Figure B8.3b. (Continued).

channel to home or the reverse searched for the nest at the correct distance over the ground (Wohlgemuth, Ronacher, and Wehner 2001). And when ants that had traveled around a bend and over a steep "hill" to find food were released on open ground, they headed in the correct direction to find the nest and searched for it at the correct distance from the release point (Grah, Wehner, and Ronacher 2005). That is, they behaved like ants that had traveled to the same feeder over flat ground, not ants that had walked the same number of steps.

The similarities between Figures B8.3a and B8.3b imply that bees and ants compute distances using essentially the same implicit countinglike process but on qualitatively different inputs. We know very little about whether and how any mammals, for example nocturnal rodents, sense distance traveled as such. Most laboratory studies of path integration in rats or hamsters test primarily its directional component: in a confined space, animals can choose which way to head but have little choice in how far to go.

Dead reckoning is a mechanism for *egocentric* spatial localization, that is, the animal is localizing things in the environment with respect to itself. *Allocentric* (or *geocentric*) mechanisms locate the animal with respect to some external frame of reference such as landmarks or environmental geometry. We have already seen one of the major disadvantages of egocentric mechanisms: if the animal is slowly "blown off course," as by the experimenter moving it, path integration does not necessarily compensate. It also accumulates error. For instance, the more the hamsters have been turned around or have turned themselves around while collecting food from the center of the hoarding arena, the less accurately they return to the nest (Etienne, Maurer, and Saucy 1988).

This makes dead reckoning most useful for comparatively brief round-trip excursions, as does the way it seems to be reset at the start of each new journey (Biegler 2000). A major advantage of dead reckoning is its availability from the first trip into a new part of the environment, before there has been time to learn reliable external cues. This makes it a potential basis for learning other cues. Dead reckoning is not only a one-trial affair, though. When hamsters repeatedly traveled in the dark on a circuitous path to a pile of food, they could still find it when forced to make a novel detour (Etienne et al. 1998), evidently using the vector computations of the dead reckoning system (Figure 8.3).

8.1.2 Beacons

In Mittelstaedt and Mittelstaedt's (1980) experiments, we might have expected odors or sounds from the nest itself to act as a *beacon* for the mother gerbil returning with a wandering pup. Beacons are sometimes referred to in the psychological literature as *proximal cues,* that is, cues close to the goal, as distinct from *distal cues,* the landmarks to be discussed in the next section. (*Local* vs. *global* cues is much the same distinction.) Often animals can use either proximal or distal cues, depending on which are available. A now-classic demonstration was devised by Morris (1981; see Figure 8.4). A rat is placed in a circular pool of water in which it swims until it finds a small dry platform, a plexiglas cylinder standing somewhere in the pool. For some rats, the cylinder is black and visible above the water. Thus the platform can function as a beacon, and because rats would rather be dry than swim, they soon learn to approach it wherever it is in the pool. For other rats, the water is made opaque by the addition of milk, and the platform is transparent and slightly below the water surface. These rats must use distal cues, objects in the room surrounding the pool, to find the platform, and they also quickly learn to approach it, provided it stays in the same place from trial to trial. When the platform is removed on test trials, these rats still head directly to the correct location and swim around it as if searching for the platform (see Figure 8.4). This behavior has typically been taken as evidence for

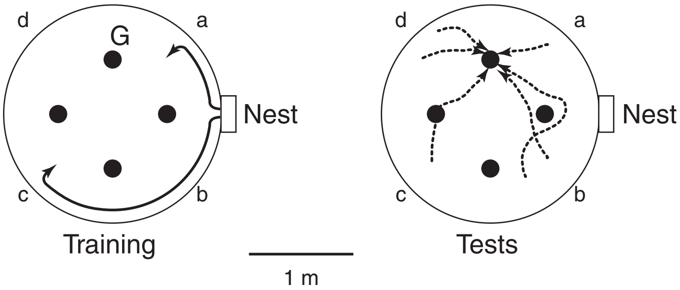


Figure 8.3. Hamsters use long-term memory of a location found by dead reckoning. In training a hamster was repeatedly lured from the nest around the edge of the arena along the two paths shown and then found its own way to the one baited cylinder (G) in darkness. In the tests animals were lured by each of the two possible paths from the nest to each of the four release sites, a–d. Subsequent paths of one hamster to the goal are shown. The paths from the familiar release sites, a and c, are only from trials with the novel path from the nest. After Etienne et al. (1998) with permission.

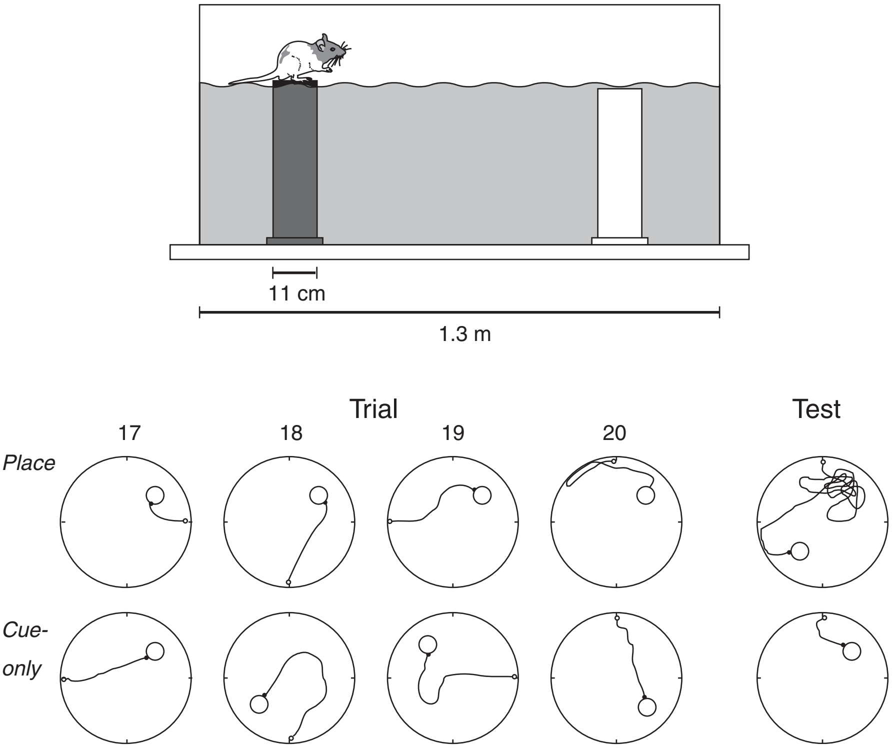


Figure 8.4. The Morris water escape task ("water maze"). At top, a cross section of the pool with a black visible platform and a white platform designed to be invisible to a swimming rat. Bottom: performance on trials 17–20 and a single test trial of one rat trained with the invisible platform always in the same place until the test ("place" condition) and one rat trained with the visible platform in a new place on each trial ("cue only" condition). After Morris (1981) with permission.

learning the specific place where the platform is, but it may often reflect instead learning what direction to head relative to distal cues (Hamilton et al. 2008).

Information from beacons is not inherently spatial because it is not vector information but rather information about value. Cues from a desired object or place, almost by definition, draw the animal to them. A classic subject in ethology is the analysis of simple mechanisms which bring this about (Fraenkel and Gunn 1961). Learned as well as unlearned features attract the animal to the goal: a fundamental effect of conditioning (Chapter 4) is that animals approach CSs associated with positive USs. For mammals, the intuition that beacons and landmarks demand different kinds of cognitive processing is supported by evidence from behavioral neuroscience (N. White and McDonald 2002). Rats with hippocampal lesions can still learn to approach a beacon like the dry platform in the swimming task, but they cannot learn tasks in which a goal is identified only by its spatial relationship to landmarks. But while finding a goal by approaching cues attached to it may be computationally simple, it has a major practical drawback: the animal must stay within range of those cues. In most natural environments, an animal that had to be able to see, smell, or hear its nest or possible food sources at all times would have its travels severely limited.

8.1.3 Landmarks

When features of a goal are not immediately perceptible from a distance, other objects in fixed locations, that is, *landmarks,* can guide the animal to it. A classic demonstration of landmark use is Tinbergen's (1932/1972) study of homing in the digger wasp (*Philanthus triangulum*). These wasps lay their eggs in a number of burrows, which they provision with bees. Each bee that a wasp collects requires a separate foraging trip, so the female wasp has to learn the location of each of her burrows. This learning takes place during a brief orientation flight. When leaving the nest for the first time, the wasp turns and faces the nest entrance and flies around in ever-increasing loops, apparently inspecting the entrance and the objects around it (Figure 8.5a). If the objects surrounding an established nest are altered while the wasp is inside, a new orientation flight will be elicited the next time she departs (T. Collett and Lehrer 1993; Lehrer 1993).

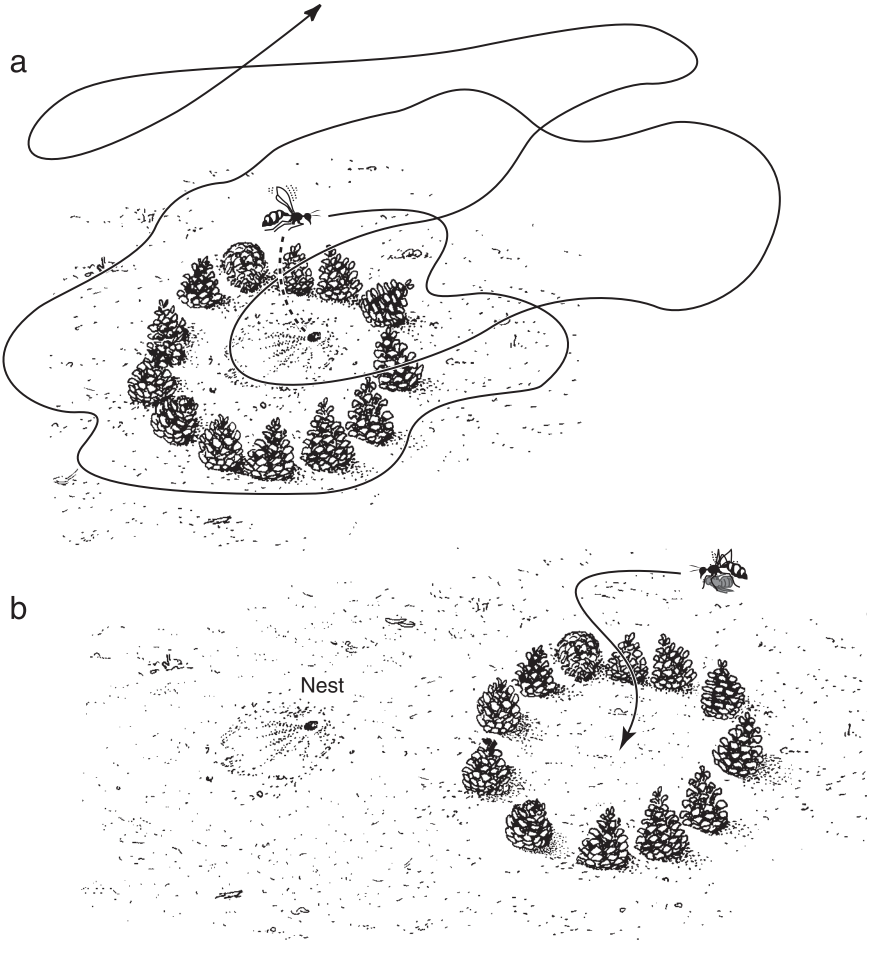


Figure 8.5. Control of orientation in the digger wasp (*Philanthus triangulum*) by nearby landmarks, a circle of pine cones. In a the wasp is shown making an orientation circle over the nest entrance before departing. After N. Tinbergen (1951) with permission.

To discover whether digger wasps were locating their nests using nearby landmarks, Tinbergen made a circle of pinecones around a nest while the wasp was inside and allowed it a number of trips in which to learn about them. Then they moved the pinecone circle to one side of the nest while the wasp was out foraging (Figure 8.5b). Although the nest entrance was still visible, returning wasps nearly always landed in the pinecone circle and searched for the nest entrance there. Only when the experimenters moved the pinecones back did she reenteer the nest. To discover which nearby landmarks the wasps learned about, Tinbergen and Kruyt (1938/1972) made landmark circles from two kinds of objects and tested the wasps with separate circles of each kind, one on each side of the nest. Wasps preferentially used as landmarks objects that were large, nearby, and three-dimensional. Such a preference makes functional sense. Large three-dimensional objects are more likely to be visible from a distance than small flat ones, and if perception of distances and directions obeys Weber's Law (Chapter 3), objects close to a goal localize it more accurately than objects farther away. Thus it is not surprising that similar preferences have been found in other animals, including European jays (*Garrulus glandularius*) (Bennett 1993) and honeybees (Cheng et al. 1987). Mechanistically, they likely reflect overshadowing during landmark learning (see Section 8.3). A landmark at a given distance supports more accurate localization the nearer it was to the goal in a training array composed of several landmarks (Goodyear and Kamil 2004).

How are landmarks used? Template matching and local views

One way to compute how to move toward a goal is to compare one's current view of the surroundings with a "snapshot" stored in memory of how the world looks from the goal. Honeybees appear to use such a mechanism. Bees were trained to find sugar water in a particular location in a laboratory room and tested with the familiar landmark array expanded or contracted. When a single landmark defining the goal's location was doubled in size, bees searched twice as far away from it as usual, that is, at the distance where the landmark would look the same as from the goal; conversely, when the landmark was half as big, bees halved the distance at which they searched (Cartwright and Collett 1983). The bee makes the matching task easier for itself by facing important landmarks in a standard compass direction, which it gets from its magnetic sense (T. Collett and Baron 1994). The animal apparently does not need to memorize how the goal looks from all directions. Chickens apparently behave similarly (Dawkins and Woodington 2000).

Figure 8.6 depicts a demonstration (Stürzl et al. 2008) that image-matching can be used to find a goal in a simple laboratory task. Food is buried in one corner of a rectangular enclosure with three black walls and one white one (panel a). Panoramic (i.e., 360°) images centered roughly at the intersection of wall and floor and taking in 115° vertically are recorded at the goal (figure 8.6b) and at other points throughout the arena. Computing the total pixel-by-pixel difference between the image at any location and the image at the goal gives a map of the arena indicating which way the creature relying on such images should move from each point to maximally reduce the difference between the current and the desired image (Figure 8.6c.) The arrows from most starting positions converge on the goal but there will be a substantial number of erroneous choices of the diagonally opposite corner, the "geometric errors" discussed in Section 8.1.5.

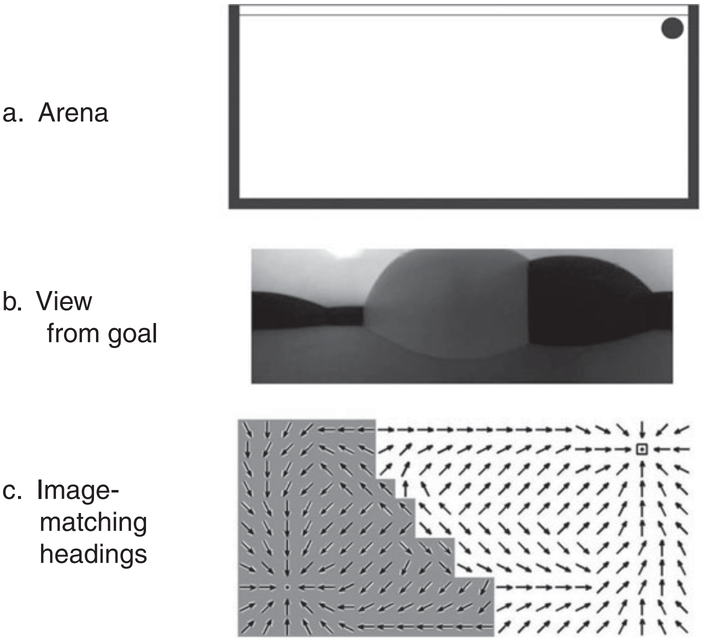


Figure 8.6. a. Rectangular arena with one white and three black walls. Black dot indicates the location of buried food (the goal). b. Panoramic image of the arena as seen from the goal (the 360° view is unwrapped with the goal corner to right of center). c. Map of predicted headings for a creature moving at each point to maximally reduce the discrepancy between the current view and that at the goal. Note that from the majority of locations a creature following the arrows will arrive at the correct corner or its geometric equivalent. After Stürzl et al. (2008) with permission.

Figure 8.6 depicts a situation in which the animal is always within sight of the goal, but animals need to get close enough to the goal to use nearby landmarks in the first place. In principle this could also be accomplished by image matching. For example, a bee could have an "album of snapshots" (Cartwright and Collett 1987) from different locations within familiar terrain, each associated with a vector from that location to the hive. In rodents, this kind of mechanism is known as the *local view hypothesis* (Leonard and McNaughton 1990) "A location is nothing more than a set or constellation of sensory/perceptual experiences, joined to others by specific movements." (Leonard and McNaughton 1990, 366; see also McNaughton, Knierim, and Wilson 1995). Navigation based on learned links between local views is in effect what goes on in experiments in which people "move around" in a virtual environment by moving a joystick to reveal sequences of views simulating what one would see when moving around a neighborhood. With experience in realistic and complex virtual environments, people can plan novel routes using the same brain areas involved in "real" navigation (Hartley, King, and Burgess 2004).

Tinbergen's wasps must have used features of the terrain beyond the nest to find their way to within sight of the pinecone circles, but if an animal encounters similar landmarks or local views in different parts of its territory, it has to know which one is which. This problem can be solved by spatial context learning or occasion setting. For example, honeybees use distant landmarks or memory of the recent route to recognize ambiguous nearby landmarks. Bees were trained to find artificial nectar in each of two small featureless huts. Within each hut, the position of the food was specified by an identical array of four landmarks, but it was on the left of the landmarks in one hut and on the right in the other. The bees learned to search in the appropriate position, apparently remembering the global spatial context (Collett and Kelber 1988).

How are landmarks used? The vector sum model

Rather than using a whole visual panorama, animals may encode information about individual landmarks. But although a single beacon is sufficient to localize a goal, a single symmetrical landmark indicates only the distance to the goal. Without directional information, it can do no better than search in a ring around the landmark. Two discriminably different landmarks unambiguously specify a single position, and an array of three of more landmarks provides redundant information. To discover how information from such multiple landmarks is combined, animals can be trained to find a goal with two or more landmarks present, and then one or more of the landmarks is moved, in a so-called transformation test (Cheng and Spetch 1998).

Sometimes animals behave as if learning about only one of several available landmarks. For example, when gerbils were trained to search between two landmarks which were then moved further apart, the gerbils concentrated their searching in two spots, each at the correct distance and direction from one of the landmarks (T. Collett, Cartwright, and Smith 1986). In contrast, pigeons trained to search in a constant location in front of a wide stripe on the wall of a large rectangular box behaved as if averaging information from the conspicuous stripe and other features of the box (Cheng 1989). When the single landmark was shifted along the wall of the box in unrewarded test trials, the position where the birds pecked most shifted along with it, but typically not as much, that is, the birds averaged information from the landmark with some other feature, possibly the corners or visible features of the room outside the box (Figure 8.7). If the landmark was moved perpendicular to the wall of the box, searching shifted toward or away from the wall, but not as much as when the landmark was moved the same distance sideways. The nearby wall of the box seemed to be weighted relatively heavily in the bird's determination of how close to the wall to search. Black-capped chickadees (Cheng and Sherry 1992) and Clarks' nutcrackers (Gould-Beierle and Kamil 1996) also behaved similarly on comparable tests.

How are landmarks used? The multiple bearings model

But what exactly is being averaged? Are whole vectors averaged or are distances and directions computed separately? Cheng (1994) found some evidence that pigeons behave as if separately computing distance and direction from a single landmark. In a natural situation with landmarks more distant than features in a typical laboratory room, directional (or *bearing*) information by itself can be used to localize a goal surprisingly precisely, as illustrated in Figure 8.8. Bearing from a landmark to a goal, as in "the big pine tree is 40° northwest of my nest," does not change with distance, whereas judgment of goal-landmark distance, following Weber's Law, is less precise for more distant objects. Moreover, even if bearings are remembered with slight error, a goal surrounded by multiple landmarks, even quite distant ones, can be localized to the small area where the remembered bearings intersect (Figure 8.8). If animals' spatial judgments reflect these properties of the world, a number of predictions follow (Kamil and Cheng 2001). For instance, when an animal has learned to find a goal that is at a certain relative position, such as in the middle, between two

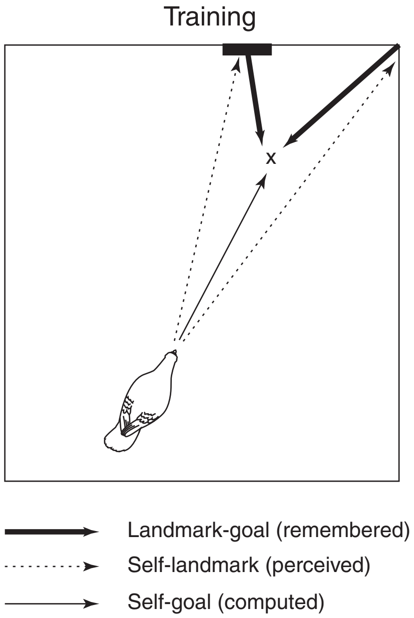


Figure 8.7. Hypothetical vectors involved in computation of the distance and direction to a goal (x) during training with a conspicuous landmark (black bar). The corner of the search space is treated as a second landmark. The self to landmark and landmark to goal vectors sum to produce the self to goal vector (the distance and direction resulting from summing two vectors is found by placing them head to tail). When the landmark is moved the animal will search somewhere along the dotted line, searching further toward the left the more heavily the black bar landmark is weighted relative to the corner of the box.

landmarks that vary in separation, direction errors should increase more slowly with interlandmark distance than distance errors.

Clark's nutcrackers are a particularly good species on which to test such predictions because they almost certainly need to rely on multiple and perhaps somewhat distant landmarks to relocate their buried caches under snow. Nutcrackers do behave as predicted by this multiple bearings hypothesis (Kamil and Cheng 2001) in several kinds of tests (Kamil and Jones 2000; Kamil and Goodyear 2001). Besides showing greater distance than direction errors, they more easily learn to locate a goal with a

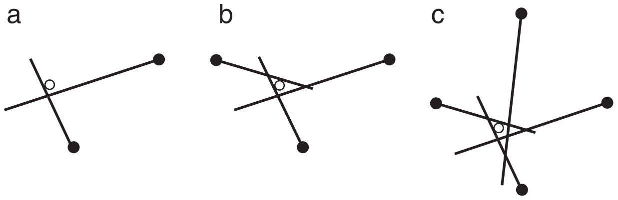


Figure 8.8. a. If an animal remembers only the compass directions (bearings) from the goal (open dot) to two landmarks and positions itself as near as possible to their intersection, even with small error in memory it can arrive reasonably close to the goal. b, c. Using more than two bearings confines search in a smaller area. After Kamil and Cheng (2001) with permission.

constant bearing to two landmarks than one at a constant distance from the line joining them. Pigeons are much less accurate than nutcrackers in laboratory tasks requiring them to use landmarks to search for buried seeds and do not show a clear difference between use of bearings and distances (Jones et al. 2002; Spetch et al. 2003). Although it is always difficult to be sure the training conditions are equated across species in such studies (but see Jones et al., 2002), the fact that this pattern of results has been found in more than one task and laboratory suggests that the nutcrackers have not only the exceptional spatial memory documented in Chapter 7 but exceptional ability at spatial localization.

A related finding that at first appeared to reflect a species difference in use of landmarks turned out instead to reflect differences in training methods. Spetch and colleagues (Spetch, Cheng, and MacDonald 1996; Spetch et al. 1997) found that pigeons trained to find the middle between two landmarks or in a square array of four landmarks in an arena or on a touchscreen behaved as if using only one landmark. When the landmarks were moved further apart in unrewarded tests, birds searched at the training distance from one of them. People behave in such tests as if they had learned "find the middle" (Figure 8.9). In this context, a report (Kamil and Jones 1997) that Clark's nutcrackers also behave as if learning a concept of middle might seem yet further evidence of the tendency of corvids to abstract concepts rather than memorize specific visual patterns as pigeons do (Mackintosh 1988). However, the pigeons in Spetch and colleagues' studies were trained with only a single interlandmark distance, whereas the nutcrackers were trained with multiple distances between the landmarks. The procedure used for the nutcrackers would be expected to teach the birds to weight both landmarks equally in determining distance, whereas relying on just one is a workable strategy for landmarks that never move. As this discussion predicts, when pigeons were trained like the nutcrackers with a variety of interlandmark distances, they also searched in the middle in the tests (Jones. et al. 2002).

8.1.4 Routes

"The animal got home because it had learned a route." As an explanation of accurate orientation, this statement is not very useful because "learning a route" can mean two different things. On the one hand, "learning a route" can refer to a mechanism of egocentric orientation in which an animal records the movements it makes in traveling between two places. This is usually referred to as *response learning* in psychology, to distinguish it from *place learning,* that is, use of landmarks. In the 1950s, considerable effort was devoted to testing whether rats learned mazes primarily as chains of responses or whether they learned about the relationships among places. Clark Hull is usually identified with the first view, and E. C. Tolman with the second. Like many controversies in psychology, this one was resolved—insofar as it ever was—by accepting that the answer to the question, "What does a rat learn in a maze?" is "It depends." Some conditions favor place learning and others, response learning (Restle 1957). Moreover, sometimes place and response learning go on in parallel and either one is used as the situation requires (Section 8.3.3).

A classic example of response learning comes from Konrad Lorenz's (1952, 109) depiction of how his pet water shrews followed their

> path-habits, as strictly bound to them as a railway engine to its tracks and as unable to deviate from them by even a few centimetres . . . . The shrews, running along the wall, were accustomed to jump on and off the stones which lay right in their path. If I

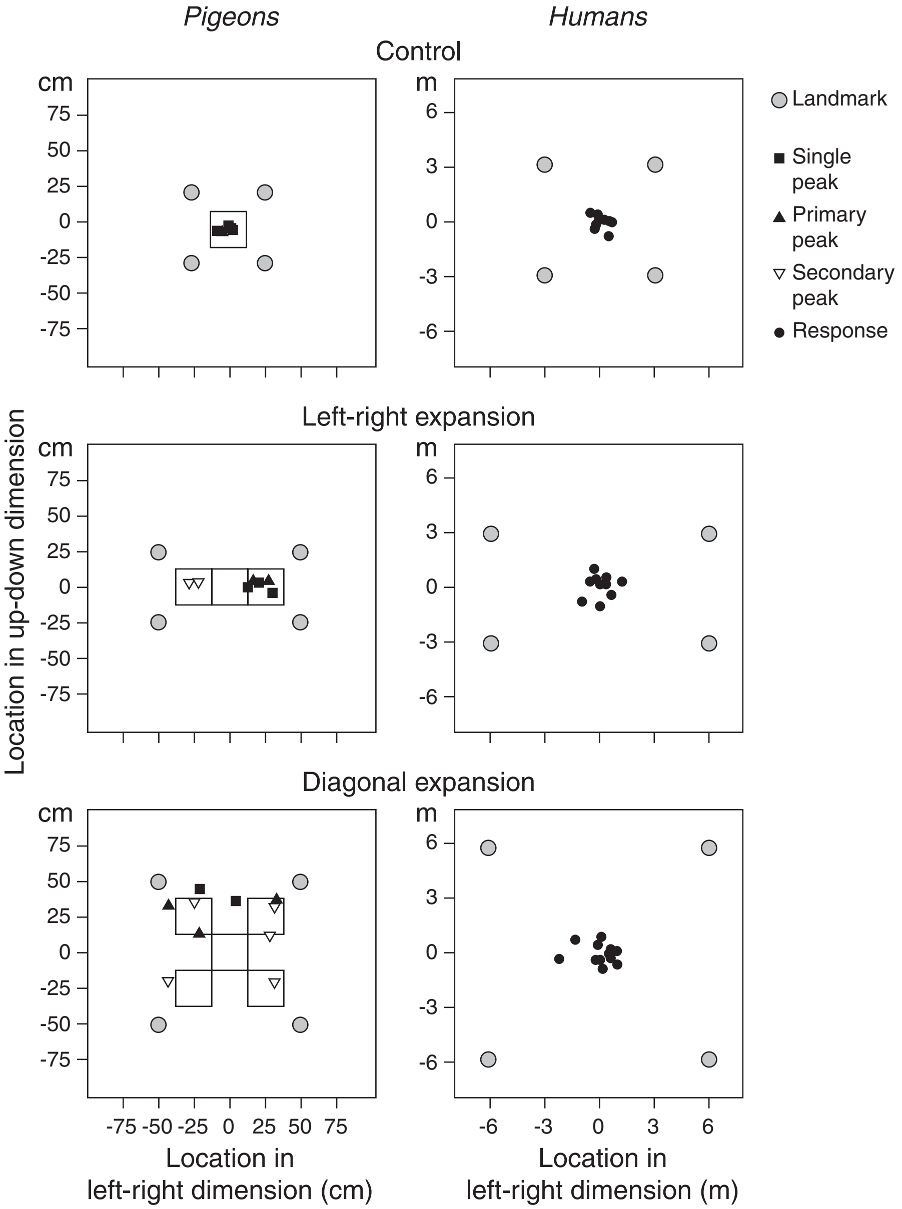


Figure 8.9. Setup and results of experiments testing how pigeons and humans use landmarks when trained to find the middle of a square array of landmarks in an open field. Redrawn from Spetch et al. (1997) with permission.

moved the stones out of the runway, . . . the shrews would jump right up into the air in the place where the stone should have been; they came down with a jarring bump, were obviously disconcerted and started whiskering cautiously left and right, just as they behaved in an unknown environment.

Gallistel (1990, 96–98) reviews analogous examples from the behavior of rats in mazes. As he points out, the animal must be keeping track of its distance and direction from the starting point (otherwise, it would not know where to jump), and it must use other cues to orient itself at the start. For the nearly blind water shrew, these must be tactile and/or olfactory cues gained by “whiskering.” The disadvantage of sacrificing continuous monitoring of the environment for speed is that changes in the environment are not detected immediately. However, as Lorenz (1952, 111) pointed out, the shrew’s brand of route learning has some advantages. It

> compensates the shrew for being nearly blind and enables it to run exceedingly fast without wasting a minute on orientation. On the other hand, it may, under unusual circumstances, lead the shrew to destruction . . . water shrews have broken their necks by jumping into a pond which had been recently drained. In spite of the possibility of such mishaps, it would be short-sighted if one were to stigmatize the water shrew as stupid because it solves the spatial problems of its daily life in quite a different way from man . . . by learning by heart every possible spatial contingency that may arise in a given territory.

In discussions of orientation in natural environments, route learning often refers to reaching a goal using a series of landmarks, that is, a series of stimulus-response (S-R) associations. This kind of orientation can be illustrated with examples of guides for hikers (O’Keefe and Nadel 1978). A person may be instructed “after crossing the bridge, turn left and proceed along the bank of the stream until you reach a hedge. Turn right and climb the hill.” Similarly, an animal may learn its way around familiar territory by memorizing distances and directions of travel with respect to landmarks. When homing pigeons are repeatedly released from the same location a few kilometers from their loft, individuals adopt different routes, but each one takes the same route time after time (Biro, Meade, and Guilford 2004; but see Wiltschko, Schiffner, and Siegmund 2007). When honeybees (F. Dyer 1994, see Section 8.3) and desert ants (T. Collett and Collett 2004) repeatedly visit the same foraging site they too learn routes with respect to landmarks in addition to using path integration (see Section 8.2.3).

8.1.5 Environmental geometry

In 1986, Ken Cheng published a remarkable discovery. He had devised a simple test of spatial working memory in which rats found food in a large rectangular box placed within a dark room, were removed from the box for about a minute and then replaced in an identical box differently oriented in the room to dig for the now-buried food. In test trials, no food was present and digging was recorded. The rats showed good memory for locations of food which they had experienced just once, in that they dug in the correct place at above chance levels. But amazingly, they dug nearly as often at the diagonally opposite point in the box like the hypothetical view-matching creature in Figure 8.6. Notice that in diagonally opposite locations the animal’s relationship to the box’s geometry is the same. For example, a short wall may be on the left, a long wall on the right. And some correlate of geometry, the box’s shape, seems to be what the rats are paying most attention to (Cheng 1986; Chapter 6 in Gallistel 1990). For if geometrically identical locations are made more discriminable, for instance by coloring one long wall white and the others black as in the enclosure depicted in Figure 8.6, the rats still make diagonal errors. Similarly, placing distinctive panels with different patterns and odors in the corners still does not eliminate the tendency to make primarily diagonal errors.

Cheng took pains to force his rats to rely on spatial cues within the boxes. They were in a dark and relatively featureless room. Testing the rat in a different box differently oriented in the room meant it could not rely on dead reckoning to return it to the same location in space after it had been removed from the first box. These conditions are crucial for control by geometry. When Cheng's experiments are repeated but with the room visible outside the box and the test and exposure boxes in the same location within the room, rats search almost exclusively in the correct location and make no more diagonal than other kinds of errors. When they are disoriented by making the room dark, not always having the exposure and test boxes in the same place, and being gently rotated between exposure and test, the same rats make as many diagonal errors as correct responses (Margules and Gallistel 1988, Experiment 3).

Cheng's (1986) findings turn out to have remarkable generality across vertebrates. Young chickens, pigeons, black-capped chickadees, two species of fish, and monkeys also encode the locations of goals relative to the geometry of an enclosure, even in the presence of features like corner panels or a colored wall that disambiguate the geometry (Cheng and Newcombe 2005). Like rats (Wall et al. 2004), these animals can eventually perform well in a reference memory task with food in the same place on every trial relative to such features. But even when a feature is the best cue to the goal, they still learn the relationship of the goal to the box's geometry, as shown by searching in geometrically correct locations when the features are removed. Geometry even takes precedence over featural information when young children are tested similarly to rats in a working memory task. Hermer and Spelke (1994) showed college students and 20-month-old toddlers the location of an object in a room and then asked them to find it after they had shut their eyes and turned themselves around ten times. If the room was white and featureless, the students and the toddlers behaved just like Cheng's rats—not surprisingly, since they had no cues to disambiguate the correct corner from its diagonal. When the room was given one blue wall, the students searched mostly in the correct place, but the toddlers were just as confused as before. Like Cheng's rats, they could be provided with salient features in the room (a teddy bear, a toy truck) that they could use for orientation, but when they were disoriented by being rotated before searching, they still fell back on purely geometric information.

By the time children are about six, they use featural cues as adults do (Cheng and Newcombe 2005). Moreover, when adults' attention is occupied with a second cognitive task during the retention interval in a test like Hermer and Spelke's, they fall back once more on geometry (Hermer-Vazquez, Spelke, and Katsnelson 1999). In Cheng's (1986) original discussion, the fact that shape of the environment seems to take priority over features of the very surfaces that define that shape was interpreted as meaning that environmental geometry is processed in a dedicated cognitive module, impenetrable to other spatial information. On this view, developmental changes in use of geometry show that although humans share the geometric module with other vertebrates, language allows them to overcome its limitations (Hermer and Spelke 1994; Wang and Spelke 2002). But the claim that language is critical here is controversial (Cheng and Newcombe 2005; Newcombe and Ratliff 2007). For example, the importance of featural cues relative to geometry depends on the size of the enclosure. Children (Learmonth et al. 2008) as well as chicks and fish are more likely to use features in a relatively large space, in some cases possibly because the features are simply larger (Chiandetti and Vallortigara 2008; N. Y. Miller 2009). Thus even if—as discussed further in the next section—most vertebrates have a geometric module, its output may be combined in adaptive ways with other information (Newcombe and Ratliff 2007).

Of course not only enclosures but also configurations of landmarks have a shape, like the linear and square arrays of landmarks in Figure 8.9. However, the animals were not disoriented in those studies so they are not strictly comparable to the studies of enclosure geometry being discussed here. The limited evidence available indicates that disoriented rats and people do not encode the shape of an array of objects as such (Wang and Spelke 2000; Skov-Rackette and Shettleworth 2005). So why should the global shape of the surrounding environment be so important, and what about it are animals encoding anyway? One answer to the first question is that sensitivity to overall geometry is a mechanism for reorientation, or getting a heading (Wang and Spelke 2002). A not uncommon experience of disorientation and reorientation occurs when one emerges from an unfamiliar subway exit into the street and does not at first know which way is which. The claim is that the overall shape of the surroundings permits reorientation, after which specific environmental features can be identified.

What is geometry?

What it is about shape that is encoded is still unclear. In a rectangular enclosure a rat could encode its position relative to a box's geometry as a certain distance from a corner with a long wall on the right and a short wall on the left. That is, it might encode comparatively local spatial information about absolute or relative (Kelly and Spetch 2001) wall lengths and their left-right position or *sense* and perhaps also the angle at which they meet (Tommasi and Polli 2004). In contrast, using more global spatial information, the animal might extract the principal axes of the space and locate the goal relative to them, for example, at one end of the long axis and to the right (Figure 8.10). (In a symmetrical shape like a rectangle, the long axis is simply the line that divides it in half lengthwise.) Testing what is used requires transforming the space in some relevant way once the animal has learned to use geometric cues.

In one such test, Pearce, Good, Jones, and McGregor (2004) trained rats to find the dry platform in one corner of a rectangular water tank and then gave them unrewarded tests in a kite-shaped tank made by taking the rectangle apart along one diagonal, flipping one of the resulting halves over and putting the enclosure back together (see figure 8.10). Thus it now had two right-angled corners, only one of which had the same

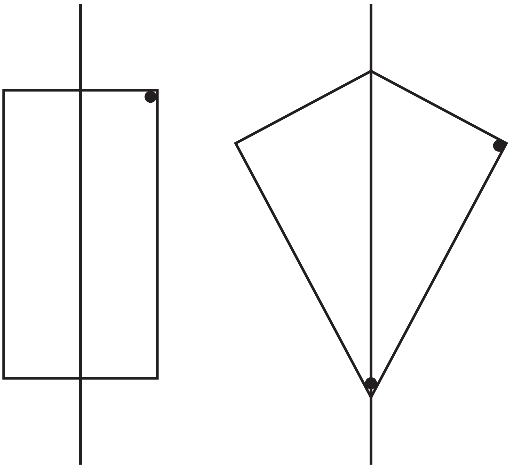


Figure 8.10. Layouts of the training (left) and testing enclosures in the experiment by Pearce et al. (2004) described in the text, showing principal axes (long vertical lines). Black dots in the kite-shaped arena indicate where rats spent most time searching for the platform in trials without the platform after training to go to the corner of the rectangle with the back dot. After Cheng and Gallistel (2005) with permission.

adjoining long and short walls with the same sense as the training corner. Much of the rats' time was spent searching for the platform in this corner, as if they had learned purely local cues. However, they searched about as much at the newly created sharp-angled corner, a finding better explained by the more global, principal axis, account (Cheng and Gallistel 2005). This latter account can also explain the results of an experiment in which young chicks were tested in transformations of a rhomboid-shaped enclosure (Tommasi and Polli 2004), although again the original authors favored a more local account of what their subjects had learned. However, local geometric features and global axes are not the only possibilities. The image matching mechanism depicted in Figure 8.6 does pretty well with several studies involving transformations of kite-shaped arenas even though it does not assume animals have any geometric information as such (Cheung et al. 2008). In summary, then, although the basic phenomena of geometry learning have proven remarkably robust, how best to account for them remains controversial (see Cheng 2008).

8.2 Modularity and integration

8.2.1 Spatial modules?

Section 8.1 makes clear that animals often have a wealth of cues for orientation available simultaneously—far and near landmarks, cues emanating from important goals (beacons), environmental shape, the *idiothetic* (self-generated or internal) cues used in path integration, memory for the chain of responses that got them from one place to another. These serve as input to distinct servomechanisms demanding different implicit computations. For instance, dead reckoning is a working memory process that takes as input some correlate of distance and direction traveled and outputs an approximation of the vector back to the starting place. The process revealed in geometry-learning experiments uses unknown parameters of the surrounding space to locate the animal relative to a global heading. Orienting by landmarks takes as input perceived self-landmark vectors and returns a vector from the current position to the remembered location of some goal. From a functional point of view then, spatial information processing consists of modular subprocesses.

But as discussed in Box 2.2, claims of modularity in the cognitive sciences are nearly always controversial because candidate modules seldom fit all Fodor's (1983) classic criteria. A debatable feature of possible spatial modules is the extent to which they are encapsulated, or impenetrable to anything other than their own specific kind of input (see e.g., Cheng and Newcombe 2005). What originally led Cheng (1986) and others (e.g., Gallistel 1990; Wang and Spelke 2002) to emphasize the modularity of spatial processing was not differences in implicit computations so much as striking observations of apparently stupid behavior in which one kind of spatial information is used to the exclusion of others that animals are manifestly sensitive to. The displaced desert ant runs right past its nest, the mother gerbil searches a blank wall even within range of the smells and cries of her babies, the water shrew jumps over a nonexistent stone, the rat turns its back on a conspicuous landmark that defines the correct corner and digs on the opposite side of the box. Such behavior suggests the animals are using one encapsulated module at a time. Indeed, in natural environments redundant cues are normally not dissociated, so relying on just one at a time is likely to work and—as with Lorenz's water shrews—may be more efficient than processing lots of cues at once. Reliance on one cue at a time may also reflect the path of evolution. More sophisticated and flexible orientation may have evolved by the addition of new modules rather than the modification of old ones. But in any case, under many circumstances animals equipped with multiple spatial modules or servomechanisms combine their outputs. In Fodorian terms, modular spatial mechanisms provide input to central decision making (Cheng 2005; Cheng and Newcombe 2005). In this section we consider ways in which multiple spatial inputs are combined to reach a decision about which way to go. A basic research strategy here is to place cues in conflict with one indicating one goal location and one, another. Does the animal search at one place, at the other, or somewhere in between? The relative weightings of different sources of information may change with the conditions. If the conflict between them is too great, animals appear to fall back on one and disregard the other. In some situations one set of cues is primary, providing a context in which other cues are used.

8.2.2 Bayesian averaging

In the vector sum model discussed in Section 8.1.3 information from two or more landmarks, that is, within one module, is averaged. However, although the example in Figure 8.7 indicates that some landmarks are weighted more heavily than others, the model does not specify how these weightings are determined. Functionally, more informative landmarks should be weighted more heavily. Elegant quantitative support for this supposition comes from human psychophysical studies investigating how two or more cues are weighted in determining perceptual localization. For example, in the *ventriloquist effect* people perceive the ventriloquist's voice coming from his puppet's mouth, as if the visual cue of a moving mouth overrides the binaural auditory cue to the location of the sound source. This phenomenon has been brought into the laboratory with stimuli consisting of a blob shown on a video screen simultaneously with a sound presented through stereo headphones, an event experienced as a ball hitting the screen (Alais and Burr 2004). Two such stimuli are briefly presented in succession, and people judge which is to the left. As one might expect, the more blurry the blob the greater the variance in judging its location when it is presented alone. More importantly, the more blurry the blob, the more combined blob+sound stimuli are localized toward the (virtual) sound source. In effect, subjects localize the bimodal stimulus at a weighted average of the locations of its components, weighting each component in inverse proportion to its variance. Such weighting on the basis of prior knowledge of probability distributions (here, "knowledge" is direct perception of fuzziness or sharpness) is prescribed by Bayes' law, according to which it is the optimal way to estimate any metric value. It applies widely in comparable situations (Cheng et al. 2007). Other aspects of Bayesian decision making are of broad interest in psychology (Chater, Tenenbaum and Yuille 2006), but they are beyond the scope of this book.

Although Bayes' Law provides quantitative functional predictions for weighting two or more information sources relevant to localizing a single goal, few data on animal landmark use are adequate to test it precisely because this requires data on the variance in judgments when each information source is presented alone (see Cheng et al. 2007). But a number of studies have provided data consistent with it. For example, on the reasonable assumption that distance judgments obey Weber's Law (i.e., their variance increases with the distance being judged), landmarks should be weighted less the further they are from a goal. An elegant illustration of this principle comes from a study of Clark's nutcrackers relocating their caches (Vander Wall 1982). Birds buried pine seeds throughout a 1.5 meter long oval arena with several prominent landmarks

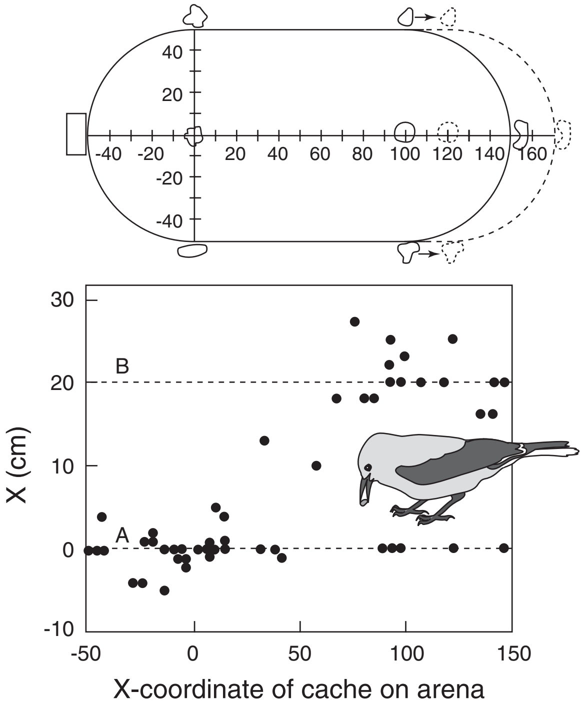


Figure 8.11. Setup and results of experiment to investigate response of Clark's nutcrackers to moved landmarks. Scale on diagram of the arena is in centimeters. Data are the distance between the location of the nutcrackers' probes for hidden seeds and the actual left-right position of the caches, as indicated on the map of the arena. Lines A and B represent, respectively, the loci of probes if the birds ignored the moved landmarks or followed them entirely. Redrawn from Vander Wall (1982) with permission.

at each end. The arena was then expanded by shifting all the landmarks at the right hand end 20 centimeters to the right (Figure 8.11). Thus caches near the right end of the arena were nearer to shifted landmarks than were caches on the left end. Birds probed farther from the stationary position of their caches and closer to a position shifted 20 centimeters the closer those caches were to the shifted landmarks. The graded effect shown in Figure 8.11, with searches in the middle of the arena shifted an intermediate distance, indicates that the moved landmarks were averaged with stationary ones, with landmarks close to a cache weighted more heavily than those further away.

Bayesian averaging should also apply when information from two spatial modules is being combined. One likely example comes from a study of honeybees in which directional information provided by a line of landmarks was put into conflict with direction given by the sun compass (Chittka and Geiger 1995). Many bees followed the landmark at displacements up to about 15°, but, as in some examples coming up next, they ignored the landmarks when they were moved too far. In Bayesian terms, averaging does not make sense if the possible positions indicated by the separate cues do not overlap because the prior probability that the goal is located between them is zero (further discussion in Cheng et al. 2007).

8.2.3 Parallel processing and hierarchical use

Rather than averaging the outputs of different spatial servomechanisms, animals may use them one at a time in a hierarchical manner. This often seems to be true when dead reckoning is involved. In numerous species and situations dead reckoning appears to be obligatory, always going on in the background and available as a backup when other cues fail, even when those cues were originally learned with reference to dead reckoning. One example comes from a study of rats by Whishaw and Tomie (1997). In a lighted room with plenty of landmarks, a rat's home cage was placed below the edge of a circular arena onto which the rat could climb and search for large food pellets which it carried back to the cage to eat. Because the cage was out of sight, rats initially had to use dead reckoning to return home, but with repeated trials from the same starting point they could learn to use landmarks as well. That this is what happened was confirmed by tests with a new starting point. In such tests, rats picked up the food and ran to the usual location of the cage with respect to landmarks. Not finding it there, they returned successfully to the new start location, using dead reckoning. Similarly, hamsters hoarding food immediately revert to dead reckoning when familiar landmarks are not visible (Etienne 2003; Etienne and Jeffery 2004). And as Figure 8.12 shows, when ants have made repeated trips home with food through a channel of a given length and are tested in shorter channels, after they emerge from the channel onto open ground they run in the direction that takes them home by dead reckoning (M. Collett et al. 1998).

As well as a backup, dead reckoning is used implicitly as a reference, in identifying landmarks in the first place (Cheng. et al. 2007). For example, hamsters hoarding food in the dark use a single small light as a landmark to return home. However, if the light is moved too far relative to the nest before the hamsters depart for the hoarding site, some of them ignore it and fall back on dead reckoning (Etienne. et al. 1990). It is as if dead reckoning leads the hamsters to expect the light in a certain position, so they disregard it when it is too far from that position, in effect treating it as a different light. Rats behave similarly (Shettleworth and Sutton 2005). Evidently a familiar landmark is recognized as such from its location with respect to the animal's internal position sense. Interestingly, if hamsters are repeatedly led astray by landmarks, they learn to rely more on dead reckoning and less on landmarks, as if recalibrating their relative weightings (Etienne 1992).

Other information about global spatial position may also determine how landmarks are used. For example, in a working memory task, black-capped chickadees learned the location of a single baited feeder in an array of four differently decorated feeders on the wall of an aviary and then searched for it later in a test of memory. When the array was moved along the wall for the test, they searched first in the feeder closest to the baited feeder's original position in the room (Brodbeck 1994). The birds

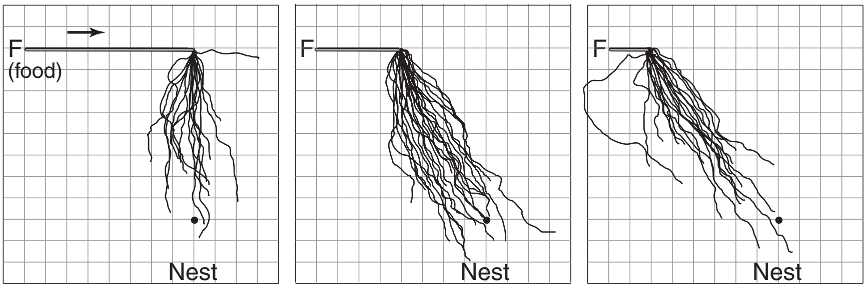


Figure 8.12. Trajectories of individual ants trained to find food at the end of an 8-meter-long channel and released at F in test channels of different lengths some distance away. Thus "nest" is the location where the nest would be relative to the beginning of the homeward trip at F in each diagram. From left to right, the test channel is 8, 4, or 2 meters long. Redrawn from Collett et al. (1998) with permission.

tended to search next in the correct position in the array of feeders. However, when the array was moved too far along the wall, performance fell to chance, as if the birds did not recognize the feeders out of their global spatial context. In the same experiment, local cues such as color on the baited feeder were occasionally placed in conflict with spatial cues by swapping the formerly baited feeder with another feeder in the array for unrewarded probe trials (Figure 8.13). The chickadees went first to the feeder in the formerly baited location, even though it now looked different. Finding no peanut there, they tended to search next in the feeder with the correct color and pattern. Much of the time, these birds used the normally redundant cues hierarchically: global spatial, local array, and color/pattern. In contrast, dark-eyed juncos, which do not store food in the wild, weight color and pattern cues about equally with spatial cues (Brodbeck 1994). The same pattern of species difference is found in an analogous operant task (Brodbeck and Shettleworth 1995) and in two other pairs of food-storing versus non-storing birds (Clayton and Krebs 1994). Analogous tests dissociating local features from spatial cues have revealed differences between men

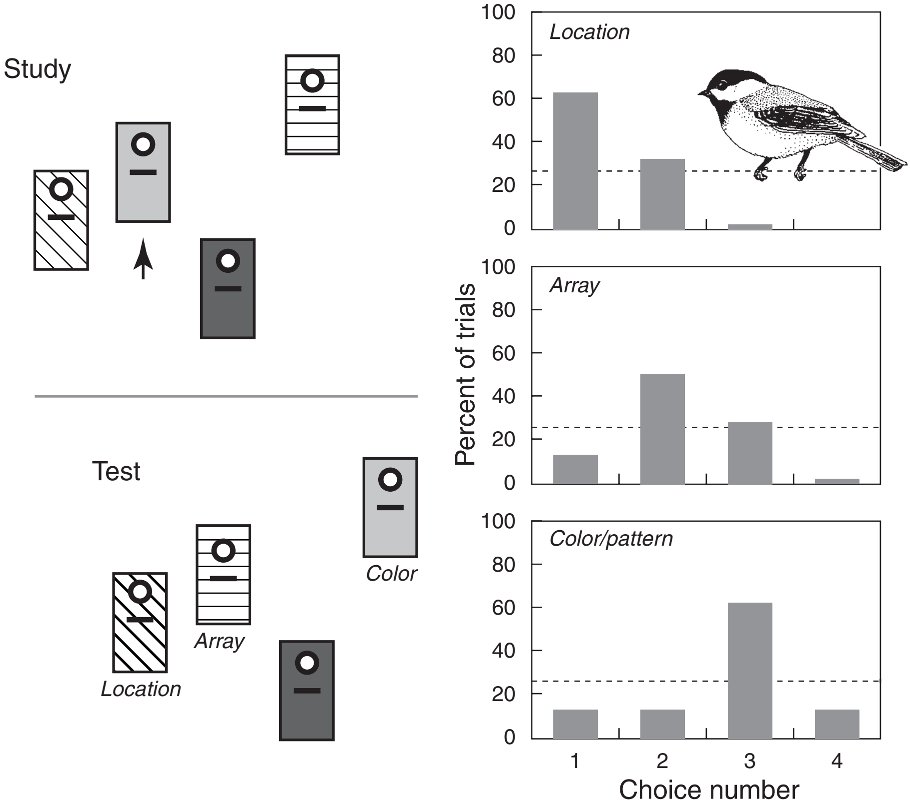


Figure 8.13. Setup and results of experiment investigating which cues to the location of reward are used by black-capped chickadees. On test trials the arrangement of feeders and their location in the room was changed as indicated between the study phase, in which the birds found and ate part of a peanut in one feeder, and the unrewarded test phase. Data are the proportion of trials in which the birds looked first, second, and so on, into the feeder in the formerly rewarded location in the room, in the same position in the array of feeders, or into the feeder of the rewarded color. Redrawn from Brodbeck (1994) with permission.

and women (Jones and Healy 2006) and between children and apes (Haun et al. 2006). Among birds, food storers' greater reliance on spatial cues may be related to their need for spatial memory in the wild (Chapter 7).

Using familiar cues in a hierarchical manner could result from learning some more strongly than others in the first place, because they overshadow other cues. For instance, perhaps chickadees use spatial cues before color cues when given a choice because they remember spatial cues better. However, although this kind of explanation may be correct for this case (Shettleworth and Westwood 2002), it is unlikely to apply in general. The examples involving dead reckoning sketched earlier in this section illustrate the more general principle that egocentric and allocentric orientation mechanisms operate in parallel (Burgess 2006). Possible parallel operation of multiple mechanisms is examined further in section 8.3.3.

8.3 Acquiring spatial knowledge: The conditions for learning

Most recent discussions of the conditions for spatial learning have been strongly influenced by O'Keefe and Nadel's (1978) claim that there is special spatial (*locale*) learning system, distinct from associative learning (the *taxon system*). The locale system is responsible for acquiring a cognitive map of the environment through exploration whereas the taxon system includes response learning, route learning, and classical conditioning, in effect all forms of associative learning. Exploration clearly does have an important role in spatial learning, as we see from research reviewed next. However, recent studies based on ideas about associative learning that largely postdate O'Keefe and Nadel's (1978) book support alternatives to the idea that all kinds of spatial information are spontaneously integrated into a unitary maplike representation.

8.3.1 Exploration

Exploration was a problem for S-R learning theory because it apparently resulted in learning without reinforcement, but in the 1960s the idea that behavior could be spontaneous and continue without reinforcement became more acceptable (Berlyne 1960; Hinde 1970a). The tendency to explore novel objects and environments is one of the best examples of special behaviors that expose animals to the conditions for learning. The rat sniffing a novel object, the young pigeon flying in circles over its loft, or the bee performing an orientation flight (Wei, Rafalko, and Dyer 2002) are actively exposing themselves to objects and spatial relationships that they need to learn about.

Spatial learning begins in the area around an animal's natal nest or burrow. A typical altricial rodent like a ground squirrel ventures out of its burrow a few weeks after birth but stays close to the entrance, maybe just rearing up and looking around from the mouth of the burrow. As the days pass, it makes longer and longer excursions around its mother's territory. Knowledge of the whole territory may be built up by connecting a series of "local charts," detailed knowledge about areas around important sites for food or refuge (see Figure 8.14; Poucet 1993). Indeed, one of the functions of territoriality may be to permit animals to acquire information that allows them to get around more safely and efficiently than they could in unfamiliar areas (Stamps 1995). For terrestrial animals, information from dead reckoning may be primary here, telling the animal where it is relative to its nest or burrow. By integrating the perceived

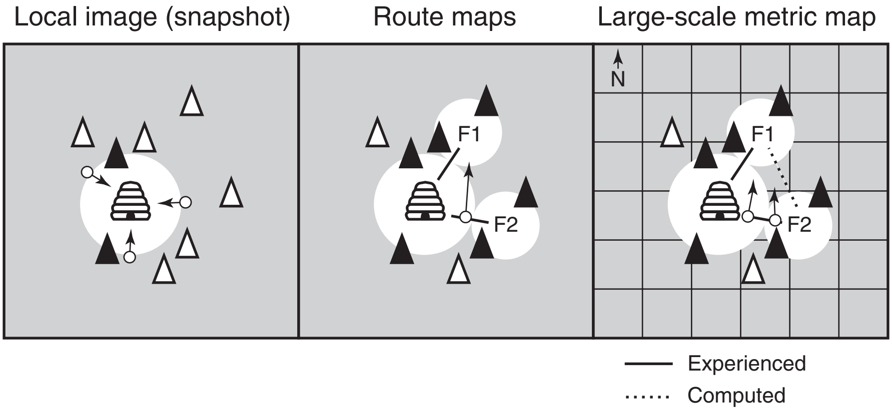


Figure 8.14. Three ways in which an animal may encode spatial information about the area around its home (the beehive). F1 and F2 are two feeding sites, the black triangles are known landmarks, and the white triangles are unknown ones. White areas are familiar to the animal; thin solid arrows are paths the animal (white dot) can take on the basis of the specified kind of representation. The grid in the large-scale map represents the idea that only in this kind of representation is information about different locations related to a common coordinate system, allowing the animal to compute a novel route (the dotted line). After F. Dyer (1996) with permission.

egocentric coordinates of prominent landmarks with this information, an animal can learn the position of nearby landmarks relative to its home (Gallistel and Cramer 1996; McNaughton et al. 1996).

The acquisition of spatial knowledge in the wild has been studied most in bees and homing pigeons. Pigeon racers have accumulated a vast fund of lore about what is necessary for the birds to learn the location of the loft (Keeton 1974; Wallraff 2005). Training racing pigeons typically begins by letting young birds fly around close to the home loft and then releasing them increasing distances away. In contrast, laboratory studies of exploration and spatial learning typically begin by dumping an animal into a completely novel environment. Even here the tendency gradually to venture further and further from a central place, presumably building up spatial knowledge, can be observed. For instance, rats placed in a large room to live travel over more and more of it in successive nights and gradually organize the space into nesting sites, food stores, runways, and latrines (Leonard and McNaughton 1990).

The two paradigms that have been used most extensively to study learning through exploration are habituation and tests of latent learning in mazes. In Chapters 5 and 7 we have seen how moving objects around, removing them, or introducing new ones elicits investigation of the altered object or location, evidence that the animals knew the features of the environment before it changed. This approach can also reveal what free-ranging animals know about their environment. For instance, wild rats ate less than usual from a familiar feeder displaced as little as a foot, showing they had learned its location quite precisely (Shorten 1954; see also Shillito 1963). And to take a rare example of spatial memory not involving food, free-ranging male thirteen-lined ground squirrels return to locations in their large (average 4.7 hectare) home ranges where they have previously encountered females. If the female has been removed, they spend longer searching for her if she had been about to go into heat the day before. The males also visit a female's territory earlier in the day when she is potentially receptive than otherwise, as if planning their route based on memory of the female's state (Schwagmeyer 1995). Male meadow voles show analogous behavior in the laboratory, with females encountered in a T-maze (Ferkin et al. 2008).

What aspects of exploration are important? Does the animal have to experience different routes through the environment, different views of it, or what? Some of the best examples of attempts to answer such questions come from studies with the Maier three-table task (Maier 1932a). This is essentially a spatial working memory task in which rats must rapidly encode the location of food in a familiar space (Figure 8.15). Three tables in a large well-decorated room are connected by a Y-shaped runway with a central platform. At the beginning of a trial, a rat is allowed to explore the whole apparatus, which is empty of food. It is then placed on the day's goal table with a large pile of food. After the rat has eaten for a few minutes but before it has depleted the food, it is placed on one of the other two tables, from which it may return and finish its meal. Trials are typically run only once a day, with the goal table changed from trial to trial. Experienced rats typically do quite well, even with delays of hours between feeding on a table and testing, but accurate choice of the goal table depends on prior opportunity to explore the maze (Maier 1932a; Stahl and Ellen 1974).

To discover whether rats can link together two parts of space they have never experienced closely together in time, Ellen, Sotere, and Wages (1984) restricted experience in the exploration phase. Three groups of rats had 15 minutes a day to explore the

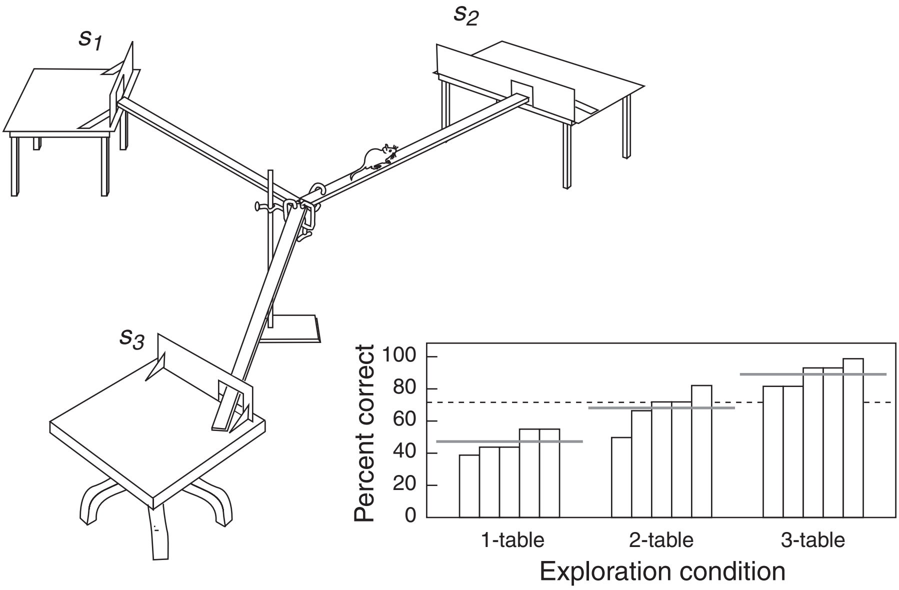


Figure 8.15. Setup for the Maier three-table task, redrawn from Maier (1932b) with permission. Screens are placed so that rats cannot see from the runways whether or not food is on any of the tables. Data redrawn with permission from the experiment of Ellen, Soteres, and Wages (1984) in which rats explored the maze piecemeal, one, two, or three tables at a time before being tested. Results are shown from five rats in each group; solid lines are group means; dotted line is performance level that could occur only 5% of the time or less.

maze, one group exploring only one runway and table per day, one exploring two different connected runways and tables, and one exploring the whole maze. Every three days, the rats were given the standard three-table test. The rats that explored only one runway at a time never performed above chance in 18 such tests, whereas rats given full exploration performed above chance from the outset (Figure 8.15). Thus the information gained from piecemeal exploration does not seem to be knitted together into a unitary representation. Other findings from mazes and swimming pools (e.g., Maier and Schneirla 1935/1964; Sutherland et al. 1987; Save et al. 1996) agree that to treat different places as connected a rat has to travel between them. Seeing they are connected is not enough. Perhaps this finding should not be surprising for an animal that normally does most of its traveling in the dark.

8.3.2 Learning about redundant cues: Competition or parallel processing?

O'Keefe and Nadel (1978) suggested that exploring novel items in a familiar space allows an animal to update its cognitive map in the same way as a cartographer adds a new farmhouse or removes a hedge from a printed map. Incorporating all available cues into a cognitive map would ensure redundancy when primary cues fail, which could be important for tasks like getting home. Indeed, an example of backup mechanisms is illustrated in Figure 8.13. As another example, experienced homing pigeons tested on sunny days use a sun compass, but birds tested under thick cloud cover can home just as well, relying on landmark memory, olfaction, magnetic information and/or infrasound (Keeton 1974). But several of O'Keefe and Nadel's ideas are contradicted by more recent findings in associative learning. One apparent contradiction is the phenomenon of *latent inhibition,* that is, mere exposure to a potential CS may retard later learning about it (Chapters 4 and 5). This is the opposite of what would be observed if the animal is continuously building a cognitive map. However, exposure to a particular spatial context does sometimes retard later learning about locations within it. Just as in associative learning, preexposure enhances discrimination (i.e., perceptual learning occurs) when the locations to be learned about are similar, but latent inhibition occurs when they are very different (Rodrigo et al. 1994; Chamizo 2003). Incorporating redundant cues into a cognitive map is also at odds with the principle of cue competition in associative learning. The Rescorla-Wagner model formalizes this principle, most clearly evidenced in the phenomena of overshadowing and blocking (Chapter 4). So do overshadowing and blocking occur in spatial learning?

Beacons and landmarks

One clear example of cue competition in spatial learning comes from a study of blocking with rats in a water tank by A. Roberts and Pearce (1999). The time spent in the quadrant of the tank where the platform was usually found was compared in two groups of rats (Figure 8.16). Both groups had been trained with a beacon attached to the platform and landmarks visible around the tank, but the blocking group were first trained with curtains drawn around the tank so they learned about the beacon alone. This initial training was expected to block learning about the added landmarks, and Figure 8.16 shows that indeed it did. Further controls with various kinds of swimming experience in the first stage still learned more about the landmarks in stage 2 than rats already trained to use the beacon.

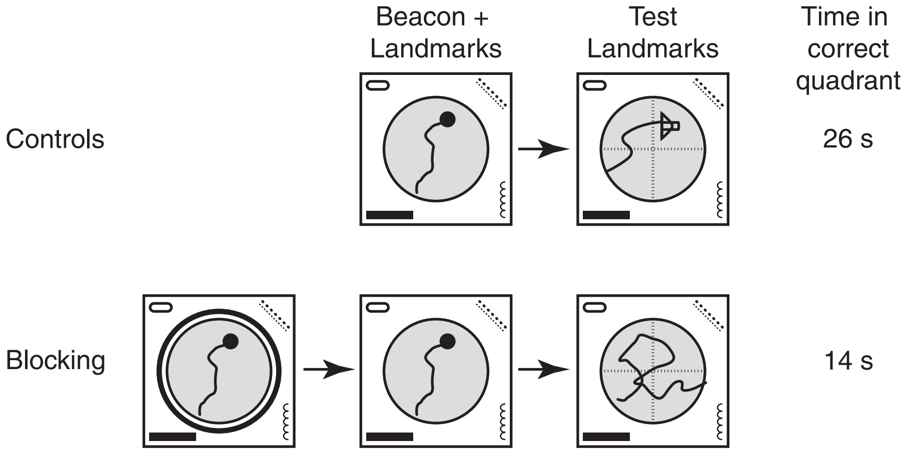


Figure 8.16. Procedure and results of A. Roberts and Pearce's (1999) test of blocking in the water tank. The heavy line around the outside of the tank represents a curtain; the black dot is the dry platform. The final test lasted 60 seconds; hence the blocking group's test score represents random search, i.e. about 1/4 of the time in the quarter of the tank with the platform.

As might be expected, landmarks closest to a goal overshadow more distant landmarks, for example in bees (Cheng et al. 1987), pigeons (Spetch 1995), and rats (Morris 1981; Redhead et al. 1997; Chamizo 2003). Landmarks can also block each other. For example, learning to use a set of three landmarks to locate the hidden platform in a swimming pool blocks rats' learning about a fourth landmark added later on (Rodrigo et al. 1997). Blocking and overshadowing have also been found between intramaze cues (floor texture) and extramaze cues (i.e., landmarks in the room) in a radial maze (Diez-Chamizo, Sterio, and Mackintosh 1985; March, Chamizo, and Mackintosh 1992). Of course such findings are not necessarily incompatible with observations of animals using normally redundant cues in a hierarchical manner. Overshadowing and blocking do not need to be complete. If some cues are simply learned more strongly than others, one would expect those learned best to be used first when available. In any case, landmarks and beacons tap only a subset of spatial processing modules. Tests of overshadowing and blocking may have different results when different spatial modules are brought into play.

Geometry and landmarks

As we saw in Section 8.1.5, when animals are disoriented relative to the outside world, they initially rely on information about the location of a goal relative to the shape of an enclosure and ignore more informative features. Some discussions of the geometric module have suggested that geometry is used for reorientation, perhaps supporting learning about features but not competing with it (e.g., Cheng 1986; Wang and Spelke 2002). That notion suggests that geometric cues should not be overshadowed or blocked by other cues. One test of this idea is illustrated in Figure 8.17. Rats were trained in a rectangular enclosure with a sawdust-filled bowl in each corner and a reward buried in the bowl near a black landmark. Rats learned to go directly to the bowl near the landmark, but they learned about geometry at the same time, as the vast majority of errors during acquisition consisted of digging in the diagonally opposite, that is, geometrically equivalent, bowl. In addition, like

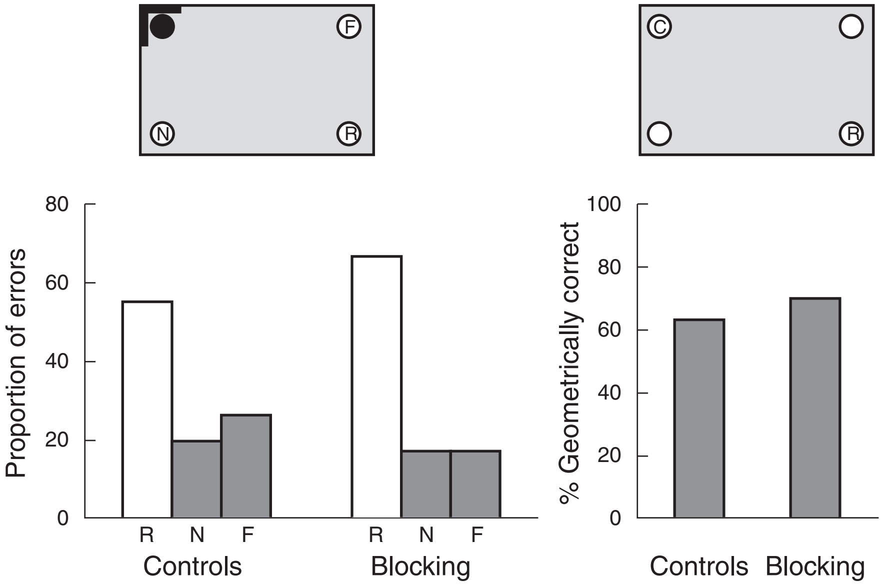


Figure 8.17 Training with a landmark (the black corner) does not block geometry learning. Rats in the blocking group were pretrained with the black corner panel in a square enclosure, yet they still made a high proportion of geometric (rotational, R) errors when transferred to a rectangle (left panel; errors summed over all of training). In a test without the landmark at the end of training, they chose the geometrically correct corners C and R, as often as controls not pretrained with the landmark (right panel). Data from Experiment 3 in Wall et al. (2004).

other species tested in a similar way (Cheng and Newcombe 2005), the rats preferred the geometrically correct corners in a test without the landmark at the end of acquisition, showing they had learned about the geometry as well as the more informative landmark. Moreover, learning based on the shape of the rectangle was not blocked by prior training with the landmark in a square (i.e., geometrically uninformative) enclosure (Wall et al. 2004).

Tests of overshadowing and blocking in water tanks of various shapes have also revealed little evidence of cue competition. Indeed, sometimes a cue at a goal facilitates learning of geometry (e.g., Pearce et al. 2001; N. Y. Miller and Shettleworth 2007). But although these findings suggest that learning the location of a goal relative to the geometry of an enclosure goes on independently of learning about its location relative to features within the enclosure, a deeper analysis reveals that cue competition is still at work (N. Y. Miller and Shettleworth 2007, 2008). Searching for a goal is an instrumental task, so the animal's choices determine the frequency with which the cues at each location searched are paired with reward or nonreward. For instance, when rats begin to learn that the salient black landmark signals reward in the situation in Figure 8.17, they start choosing the marked corner more often. When they do choose that corner they also experience a pairing of its geometry with reward. The learning based on these pairings is reflected both in the relatively large proportion of geometric errors early in training and in geometrically correct choices during tests without the landmark. The same process leads the blocking group to learn about the geometry of the rectangle. Geometry and features are competing for learning, but this is typically not evident in choices because if a location is chosen on the basis of the total associative strength of its cues relative to the total at all locations, one location can be quite strongly preferred over the others even while none of the individual cues is at asymptote. For example, the corner by a landmark in a square enclosure can be chosen a large proportion of the time even if its associative strength is not high enough to block geometric cues when transferred to the rectangle. One prediction of this model, then, is that conventional cue competition will reveal itself in choices under some conditions, including after prolonged training in either stage of an experiment like that in Figure 8.17. The shape of the enclosure and the distribution of features within it will also influence the results, as indeed it does (Miller and Shettleworth 2007).

Dead reckoning and beacons

The characterization of dead reckoning as an obligatory process, a basis for learning the locations of stable allocentric cues yet always going on in the background implies that the idiothetic cues for dead reckoning do not compete with learning landmarks and/or beacons. Indeed, if they did how would animals ever learn about stable allocentric cues? But although some of the findings described in Section 8.2.3 imply that dead reckoning operates independently of beacon and landmark learning, only one study (Shettleworth and Sutton 2005) has tested this implication with a study of overshadowing and blocking. Rats found food pellets in a large circular arena and carried them back to eat in a home cage that was concealed behind one of 16 identical doors on the periphery of the arena. In some conditions the correct door was surrounded by a black panel, functioning as a beacon, and in other conditions no exteroceptive cue identified it so the rats had to home by dead reckoning. To ensure that the rats could not locate the home on the basis of cues outside the arena, the home cage and black panel were in varying locations in absolute space, and the rats were disoriented before entering the arena. Rats trained with the beacon homed no more accurately than rats trained with a “beacon” at random locations relative to the home door, and the two groups homed equally accurately in tests without the beacon. That is, beacon learning did not overshadow the cues used in dead reckoning. And as might be expected on functional grounds, rats that already had extensive experience homing on the basis of dead reckoning alone learned as much about the beacon when it was added as rats that had it from the outset, that is, dead reckoning did not block beacon learning.

Places and responses

Extensive literature also points to a noncompetitive interaction between spatial learning systems in the case of “place” (or landmark) and response learning (sometimes referred to in this context as *habit* learning). Figure 8.18 shows a classic setup for testing whether rats that learn to make a particular turning response to arrive at a particular place in a T-maze have learned the response or the place. Notice, however, that the test consists of forcing the rat to choose between making the rewarded response and going to the rewarded place. A choice consistent with one kind of learning does not mean that the other kind has not also occurred. The typical finding in such tests is that early in acquisition place learning is evident, but later the habitual response prevails (Restle 1957; Packard and McGaugh 1996). This finding in itself suggests cue competition is not going on. If it was, how could response learning develop when place learning was already allowing the animal to locate the reward? Neurobiological data also lend support to the idea that rather than competing, place

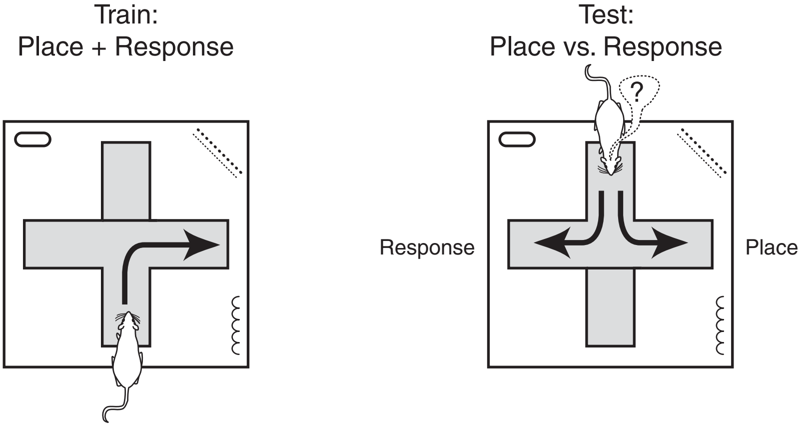


Figure 8.18. Test of whether rats trained in a T maze as indicated in the left panel learn where to find reward or what response to make. The two possibilities are dissociated as indicated in the setup on the right. The dark bar is a block that confines the rat to one part of the maze. The random shapes around the edge are objects in the room that can serve as landmarks.

and response learning go on in parallel, in different brain regions, the hippocampus and caudate nucleus respectively (White and McDonald 2002).

This was beautifully demonstrated in a study using a setup like that depicted in Figure 8.18 in which rats were given the place versus response test early or late in place + response training and while the hippocampus or caudate was temporarily disabled with injections of lidocaine (Packard and McGaugh 1996). Rats with the hippocampal place-learning system disabled chose randomly in the early test but chose on the basis of the trained response in the later test, consistent with the observation that response learning emerges gradually. In contrast, rats with the caudate habit system disabled chose the rewarded place in both the early and late tests. Thus response learning did not emerge at the expense of place learning: it remained intact and could be revealed when the competing behavioral tendency was removed. The same issue was addressed without pharmacological manipulations by testing rats in a radial maze arranged so that response learning and place learning could be dissociated (Gibson and Shettleworth 2005). The results suggested that prior response learning interferes with learning about landmark (place) cues introduced later. This may have occurred because rats for which a habitual response continues to lead to reward when place cues are added simply pay less attention to, or spend less time exposed to, those cues than controls.

Redundant cues in spatial learning: Conclusions

The picture of spatial learning sketched here is not that of a single system in which cues compete for a limited amount of predictive value like CSs in conditioning. Landmarks compete for learning with beacons and geometric cues and with each other, but dead reckoning goes on in parallel yet somehow in support of learning about allocentric cues. At least in mammals, response or habit learning is another parallel system. The existence of parallel systems allows for the redundancy which functional considerations suggest is particularly important for spatial tasks like getting home. Ultimately whether different mechanisms evolve so as to compete would be expected to reflect the relative costs and benefits of relying on minimal sufficient predictors versus processing redundant information. In addition, the costs and benefits of any one mechanism may be balanced by the costs and benefits of others. For instance, well-learned responses demand little attention and permit fast travel in familiar places, but a slower, more attention demanding system such as exploration and landmark learning is called for when conditions change. Evolutionary pressure to optimize over different criteria may account for the widespread existence of multiple spatial learning systems. Whether the multiple kinds of memories that result are integrated into a cognitive map in any sense is the question for the next section.

8.4 Do animals have cognitive maps?

8.4.1 What is a cognitive map?

In Chapter 4, "How does the animal represent the CS?" meant simply, "What features of the CS are encoded or remembered?," a rather minimal kind of representation. In contrast, the representation embodied in a cognitive map is typically assumed to encode distances and directions and to enable mental operations on them. To take an example we will shortly consider in more detail, an animal that can encode the distance and direction of two feeding sites from a home base and whose nervous system is capable of implicit computations analogous to the operations of vector algebra can move directly between the two feeding sites without going home in between (Figure 8.14, "metric map").

Distances and directions are the *metric properties* of space. Blueprints, city plans, road maps, and globes are useful because they represent distances and directions accurately. But plenty of useful maps do not preserve such vector information. A familiar example is a subway route map. Such a map is useful for planning a trip on the subway because it shows which station is on which route and what order they can be reached in. Such a *network map* can be used without its representing distances between stations or angles between connecting routes. Indeed, because these may not be represented accurately, a tourist wanting to explore the city on foot would be foolish to use a it as a guide. In contrast to the subway map, a map that preserves distance and direction information, a *vector* map, allows the planning of novel routes to unseen goals. How useful it is, though, depends on the density of identifiable locations represented. For example, a tourist starting from an obscure side street armed only with a vector map of the city landmarks has to wander around until finding a place marked on the map. This potential limitation of real Euclidean paper maps has traditionally been overlooked. It is an assumed unlimited flexibility that has distinguished a cognitive map from "mere" reliance on one or more kinds of spatial cues. As Section 8.2 shows, however, single cues or combinations of them can guide animals very effectively. This means that it is almost impossible to find indisputable evidence that any animal is using a cognitive map in the sense of a global representation of space equivalent to an overhead view that preserves distances and directions among an infinity of locations. Whether *cognitive map* always means the same thing is a problem too, as we see by surveying some of the landmarks in its history.

Tolman

E.C. Tolman introduced the term *cognitive map* into psychologists' debate about place versus response learning. Rather than simply acquiring chains of stimulus-response connections, Tolman claimed, rats in mazes acquire "something like a field map of the environment" (Tolman 1948, 192). Stimuli influence behavior not through S-R connections, but through the mediation of the cognitive map. Cognitive maps could be broad and comprehensive or "narrow strip maps," confined to knowledge of specific routes. The most compelling data Tolman cited in support of his hypothesis were from tests of *latent learning* and ability to take novel shortcuts in mazes. In a typical latent learning experiment, a rat was allowed to explore a maze without receiving any reward. For instance, food might always be present in one location but the rat would be satiated. If the rat ran straight to the food when it was hungry later on, its behavior could not have resulted from the reinforcement of S-R connections because it had not been getting any reinforcement. Therefore, it must have learned the location of the food and generated appropriate behavior on the basis of this knowledge. Similarly, an animal that took an efficient novel shortcut when displaced to a new location or when its usual path to a goal was blocked must have acquired knowledge about the goal as a place.

Much of the behavior just described is now largely taken for granted in the view of conditioning as a representational process described in Chapter 4, so in a sense Tolman's view of learning as S-S connections has prevailed. It is no longer problematical, for instance, that animals approach or avoid places on the basis of knowledge about their value. Indeed, this is the basis of the popular *conditioned place preference* test. In this paradigm an animal is first exposed to each of two distinctive chambers in each of which a different biologically significant event occurs, for example food in a grey square chamber and opportunity to run in a wheel in a striped round chamber. The relative value it gives to them is then measured by removing the rewards, connecting the two chambers and seeing where the animal spends more time. And in at least some of Tolman's experiments, tests of rats' specifically spatial knowledge did not go beyond demonstrating such S-S learning. For instance, if cues near the goal were still visible from a novel starting point, rats could approach them without any maplike knowledge, as in the experimental arrangement depicted in Figure 8.19 (Tolman, Ritchie, and Kalish 1946).

O'Keefe and Nadel

Although Tolman's views are important in the history of psychology, he actually said rather little about the properties of cognitive maps and how they might be acquired. After a lapse of 30 years, this gap began to be filled by John O'Keefe and Lynn Nadel (1978) in their influential book *The Hippocampus as a Cognitive Map*. They developed the view that some organisms, including humans, rats, and migratory birds, possess cognitive maps, in the sense of a unitary, allocentric, connected spatial representation in which experience locates objects and events. Acquisition and use of the cognitive map is supported by the locale system, a cognitive module located in the hippocampus of vertebrates. The locale system contrasts with the taxon system, which supports conditioning and is located elsewhere in the vertebrate brain. The learning supported by the taxon system was seen by O'Keefe and Nadel as relatively inflexible compared to that supported by the locale system, but developments in the last 30 years have undercut this distinction. As in Tolman's account, maps are acquired through exploration (latent learning) and allow more flexible behavior than route learning. However, as in the example mentioned above, some flexibility can result from stimulus generalization, and at least over relatively short distances, path integration allows

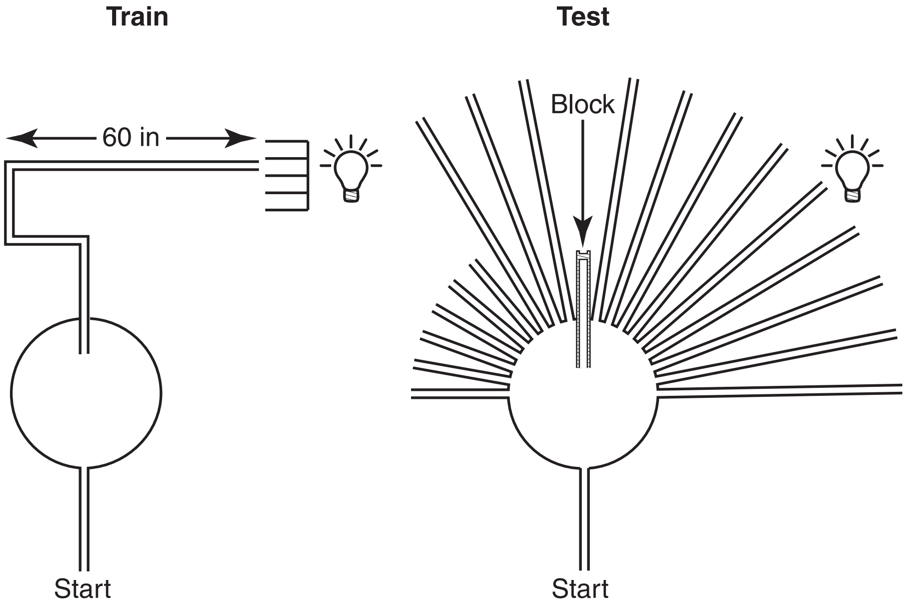


Figure 8.19. Setup used by Tolman, Ritchie, and Kalish (1946) to test place learning in rats. The alleys were arranged as shown on the left for training; for testing they were replaced with the "sunburst" maze shown on the right. Rats tended to choose the new path that led directly toward the goal. Note the light at the goal box. Redrawn from Tolman et al. (1946) with permission.

travel toward unseen goals in a way not fully appreciated when O'Keefe and Nadel first wrote.

Gallistel

Gallistel's (1990) review of spatial behavior in animals has a very different flavor from O'Keefe and Nadel's, partly because by 1990 the cognitive revolution in psychology had made the notion of cognitive mapping more acceptable. In addition, this period witnessed an explosion of relevant research, and Gallistel was the first person writing for people in the cognitive sciences to bring together the new laboratory studies on rats in the Morris swim task and radial maze with biological field work on bees, ants, homing pigeons, and other animals. This integrative approach has been tremendously influential and is now almost taken for granted, as can be seen in numerous more recent reviews (e.g., Newcombe and Huttenlocher 2000; T. Collett 2002; Jeffery 2003). Gallistel's (1990) definition of *cognitive map* is fairly loose (e.g., Chapter 6, 121): any orientation based on implicitly computing distances and directions is evidence of a cognitive map. Dead reckoning, matching "snapshots," or responding to landmarks all count as cognitive mapping, albeit perhaps in a small-scale and limited way. Species may differ in the richness and detail of their cognitive maps, but evidence for them is ubiquitous.

Bennett

Because *cognitive map* means different things to different people and because most frequently used behavioral assays of cognitive mapping have not ruled out well-defined alternatives such as dead reckoning or generalization from familiar local views, it is almost impossible to find unambiguous evidence for it. Discussion of cognitive maps should be replaced with better-grounded specification of how animals (including people) find their way from place to place. This position was stated forcefully by Bennett (1996) and echoed by Mackintosh (2002) in an article titled, "Do not ask whether they have a cognitive map but how they find their way about." To see why this is good advice we need to review the approaches to testing for cognitive maps.

8.4.2 Mapping and short-range orientation

Shortcutting

A central behavioral prediction from any notion of cognitive mapping is that within familiar terrain an animal with a cognitive map should be able to reach a goal by a novel route. It will take a novel shortcut when one is made available, and if it is displaced to a new starting place it will head directly to the goal rather than returning to the familiar start before continuing its journey. Tests of this prediction have a long history, beginning with the work of Tolman, Ritchie, and Kalish (1946) illustrated in Figure 8.19. In laboratory studies like theirs it is easy to guarantee that the offered shortcut is novel, but it is not so easy to be sure that animals are doing anything other than orienting by landmarks (and indeed, that rats use landmarks rather than only S-R habits may have been all that Tolman aimed to establish). As long as landmarks visible from the goal are visible to the animal in the same left-right relationship at the point where it chooses between the shortcut and some other route, the self-to-goal vector computed as in Figure 8.7 will take the animal along the more direct route. Cues at the goal clearly influenced the rats in Tolman et al.'s (1946) original study, because there was a distinctive light right at the goal box (see also Chapuis, Durup, and Thinus-Blanc 1987). In a careful study in which dogs often took the shortest route between two novel locations in a large field (Chapuis and Varlet 1987), this could have been a problem too. The dogs were led first to one location and then another and shown meat in each one before being released from the common starting place for these trips to find the food. As they were shown each piece of food they could have encoded its location with respect to features in the surrounding familiar environment. Indeed, rats can acquire new knowledge about what is where in a single trial in an environment which already supports a network of associations (Tse et al. 2007).

These considerations mean that to test whether animals are using a representation that includes more than local landmark-goal vectors, landmarks perceptible from the goal must not be perceptible when the shortcut is chosen. The importance of this requirement is very well illustrated by a much-discussed series of studies with honeybees. Honeybees are ideal subjects for studies of spatial orientation in natural landscapes because foragers routinely make many round trips each day between the hive and feeding sites hundreds of meters away. Using methods pioneered by Karl von Frisch (1967), marked individuals can be trained to artificial feeding sites selected by the experimenter. Newly emerged foragers gradually become familiar with the area around the hive, as shown by the observation that when bees are released some distance from the hive, the experienced individuals are more likely to find their way back (review in Dyer 1994). Extensive and detailed spatial knowledge thus seems to exist in bees' tiny brains. Discussion of whether it can be described as a cognitive map has centered around a shortcut experiment originally reported by Gould (1986) and repeated by others, sometimes with different results (Wehner and Menzel 1990; F. Dyer 1991, 1994). Bees were trained to only one of two feeders, F1 and F2, equidistant from the hive but out of direct sight of each other. The lines connecting A, B, and the hive formed an approximately equilateral triangle, as in the arrangement depicted in Figure 8.14. The test of whether the bees knew the relationship of a feeding site to the landscape as a whole consisted of capturing marked individuals as they left the hive for one site, say F2, and releasing them at the other. A bee released at a novel location flies up maybe 9 or 10 meters, circling around as if getting its bearings, and then heads off in a definite direction. Data in these studies thus consisted of the compass bearing recorded for each bee when it vanished from view.

Because when tested Gould's bees tended to head toward the site they had been trained to, he concluded that the bees had a "maplike representation" of their local environment. But because their experience was not controlled, it is impossible to know whether the shortcut was truly novel. Moreover, when the bees flew up to get their bearings they could have gotten a view of the landscape sufficiently similar to that near the familiar feeding site to allow them to orient. And indeed, "maplike" orientation in such a test does seem to require this, as shown by Dyer (1991) in a similar study that had one important difference. One of the two critical feeding sites, B, was down in a quarry whereas A was up at the same elevation as the hive. Bees trained to B, in the quarry, and released at A behaved like Gould's bees and headed off from the novel release site toward the feeding site B. But bees trained to feed at A, on the high ground, and released at B, in the quarry, could not easily get a view similar to that which they saw when leaving the hive for A. These bees did not head either for the hive or for A but departed from B in the same compass direction they had been taking when they left the hive. This did not reflect some peculiarity of site B in the quarry; bees trained to fly directly between A and B were able to orient accurately.

As we see presently, this is not the end of the story of cognitive mapping in bees, but Dyer's study remains an important demonstration of why tests of shortcutting must ensure that cues at the goal are not perceptible at the choice point. This was done for rats in the enclosed maze depicted in Figure 8.20 (Singer, Abroms, and Zentall 2006). The three goal boxes were identical, but each arm had a distinctive

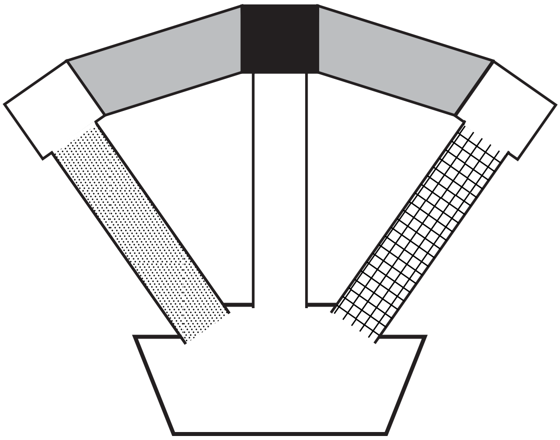


Figure 8.20. The enclosed maze used by Singer, Abroms, and Zentall (2006) to test cognitive mapping in rats. Different shadings signify different textures in the maze arms. The arms linking the three goal boxes (top of the figure) were open only for testing. Redrawn from Singer, Abroms, and Zentall (2006) with permission.

floor covering. Rats found chocolate in the center goal box, and a piece of cereal in a constant one of the side goal boxes. The maze was rotated within the room from day to day to prevent use of extra-maze cues, and food odors within the goal boxes were also controlled. Rats were trained until they visited the two baited arms first on more than 90% of trials and then tested with only the center arm open to the start box and, for the first time, alleys open between the center and side goal boxes. On the first test 15 of 20 rats chose the novel alley to the baited side, and rats continued to choose at above-chance levels over 8 further tests. In an experiment conducted in the same way except that the alleys were unlined and both baited goal boxes had the same food, rats did not perform above chance in the tests, indicating that performance is not based entirely on dead reckoning within the maze. In a more extensive study W. Roberts, Cruz, and Tremblay (2007) found comparable results with an enclosed four-arm maze.

Singer and colleagues suggest that the rats must have had a cognitive map of the maze, but what exactly can "mapping" mean here? In both their study and that of Roberts and colleagues (2007) distinctive cues in the arms or goal boxes identified locations in the maze. We have already seen (Section 8.2) that dead reckoning can be used to locate a familiar goal by a novel route, and that it can be reset by exposure to familiar landmarks (e.g., the distinctive floor and/or food). The experimental design ensured that rats had to base their choices on their internal position sense, and once they were going directly between two arms, they had ample experience of their relative positions based on idiothetic cues. Thus, considering the cues available allows reference to mapping to be replaced with consideration of how specific cues are used in concert.

Planning ahead and taking detours

Shortcutting is but one test of whether animals have an overall map of a familiar environment. Detouring when the shortest route is blocked and choosing an efficient path among multiple goals are two equally classic tests of cognitive mapping. In an example of the latter, Emil Menzel (1978) showed chimpanzees the locations of up to 18 pieces of food in a large outdoor enclosure. The chimpanzee tested was carried around by one experimenter while another hid the food. Other members of the social group, serving as controls for possible influences of olfactory cues or general knowledge of the experimental space, watched from a nearby cage. When all the animals were released into the enclosure shortly afterward, the one that had observed the food being hidden went around collecting it. The animals did not necessarily follow the same path they had been carried along while the food was being hidden nor move at random among the food sites, but took a fairly efficient route. When this tendency was tested with just four or five sites, two or three on one side of the enclosure and the remainder on the other, animals visited the side with most food first in 13 out of 16 cases (Figure 8.21a). However, 13/16 does not differ significantly from the 9.6/16 expected from random choice with 60% of the food on one side. Similarly, marsh tits (*Parus palustris*) do not retrieve seeds stored in an aviary in the order in which they stored them, nor do they retrace the path that they took while storing (Shettleworth and Krebs 1982). But an efficient route need not mean the animal has a representation of the environment as a whole and plans its entire trip within it. Whenever features defining different goals are within sight of each other, the animal will likely approach the nearest or most valuable, making local choices, one at a time, based on currently perceptible cues.

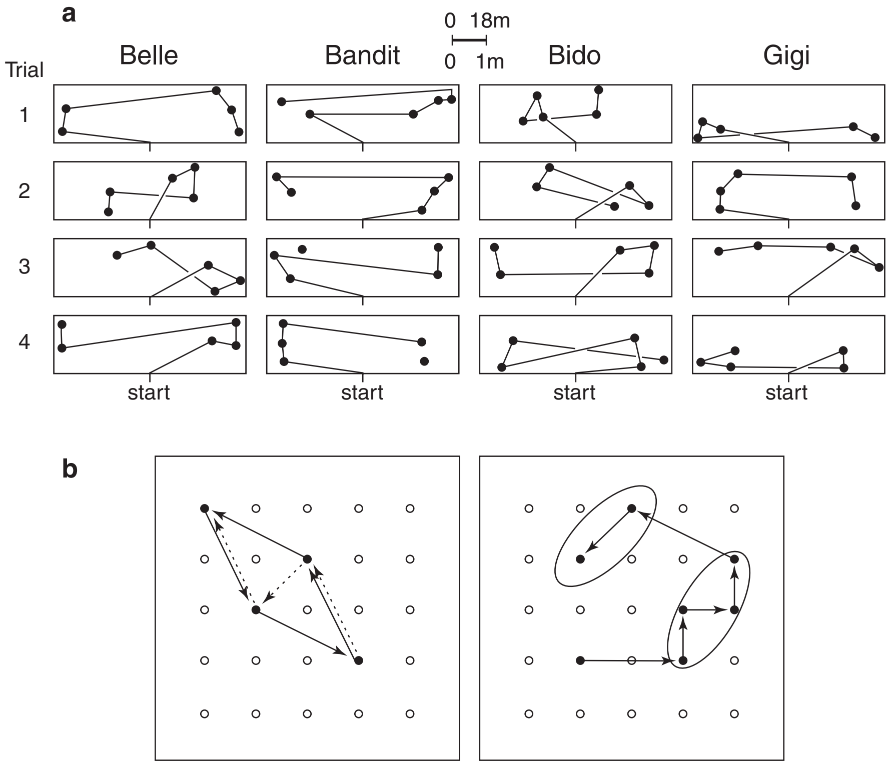


Figure 8.21. a. Paths taken by each of four chimpanzees in their first four trials with five hidden food items. Redrawn from E. Menzel (1978) with permission. The marker indicates the scale in both a and b. b. "Diamond" and "unequal sides" configurations used for testing spatial planning by vervet monkeys. In the diamond configuration, the shortest path among all four corners is the dotted one if the animal is not planning to return to the start (lower right vertex) but the black route if it is. Redrawn from Gallistel and Cramer (1996) with permission.

Nevertheless, cognitive mapping (or at least planning a route beyond the next move) can in principle be distinguished from wholly local choices with certain arrangements of sites. For example, the optimal path for collecting food from the diamond-shaped arrangement shown in Figure 8.21b depends on whether the animal is going to return to the starting point. The animal can make the optimal choice after the second food item only by planning beyond the next two choices. Similarly, when four food items are on one side of an arena and two on the other, the animal must mentally look beyond the first two items to be collected in order to move optimally. Cramer and Gallistel (, 1997; Gallistel and Cramer 1996) report that vervet monkeys behaved as if planning routes in both of these tests. However, without knowing the animals' reinforcement histories in the testing situation, which are not reported, it is difficult to know how to evaluate these data. Moreover, in the four- versus two-item test, the monkeys might simply have remembered the area with four items better if they spent more time there while the sites were being baited. Nevertheless, this approach could be pursued further than it has been (see also Janson 2000).

Some species of jumping spiders are well known for their ability to choose efficient routes and detours in natural conditions. These spiders do not weave a web but pursue their insect prey visually, sometimes watching a victim for a long time while slowly creeping up on it. The spider might move away from the prey initially and climb up a branch from which it can pounce. Tarsitano and Andrew (1999) captured this situation in the laboratory by placing a spider (*Portia labiata*) in the middle of a square enclosure where it could see a prey item above and in front of it. To reach the prey, the spider had to walk diagonally away from it, climb a pole, and traverse a series of two ramps. When spiders were confronted with a choice between two such routes, one to each side, and one of them had a gap in it, 16 of 18 spiders headed in the direction of the unbroken path as soon as they left the start platform. When both routes were complete, they chose the one they had scanned the most while sitting on the start platform; when one route was incomplete, simple algorithms describing scanning ensured they spent most time scanning the complete one. Like the ants we meet shortly, the spiders provide a nice illustration of how apparently demanding feats of navigation can be accomplished by simple mechanisms (see also Cheng 2006).

Knitting together

The idea that animals orient with reference to a cognitive map implies that information gathered in different parts of a journey, even qualitatively different kinds of information, is knitted together into a single allocentric representation. Unlike in the examples of integrating simultaneous cues in Section 8.2, here cues are encountered successively. This occurs in a setup developed by Benhamou (1996) for rats in a water tank and subsequently adopted by Gibson and Kamil (2001; Gibson 2001) for Clark's nutcrackers and people (Figure 8.22). The subject's task is to find a goal hidden at a fixed location in a room full of landmarks. The subject encounters the landmarks on the first part of the

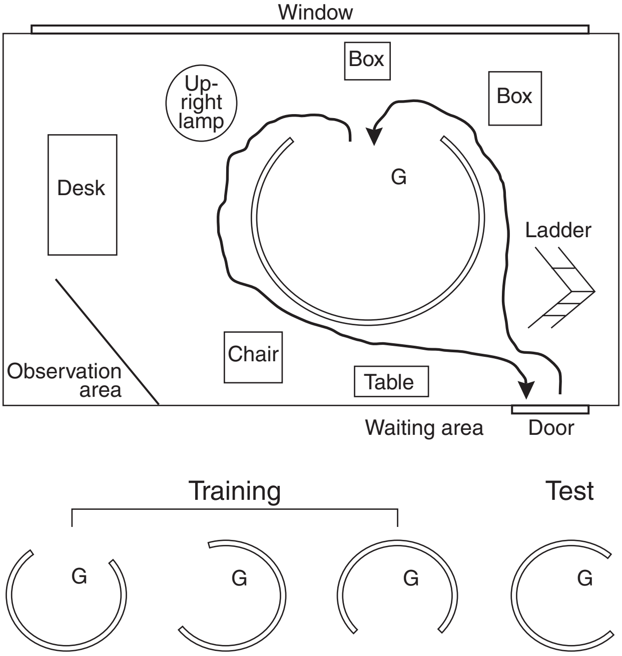


Figure 8.22. Overhead view of the setup used by B. Gibson (2001) to test cognitive mapping in people. The semicircle indicates the opaque enclosure within which the goal (G) was located. The enclosure was rotated from trial to trial to allow about a 270° view of the room from the goal in total. Three of the positions used are shown below the diagram, along with the orientation used for the test. The arrows are the paths people used to enter and leave the enclosure. Redrawn from B. M. Gibson (2001) with permission.

journey, but the goal is within an enclosure that permits only about a 90° view of the room. This enclosure is rotated from trial to trial, so that its entrance has no consistent relationship to the goal, and so that over trials the subject sees different parts of the landmark panorama from the goal. Once subjects can find the goal they are tested with the enclosure in a novel orientation, so they have a new view of landmarks from within it. Neither rats nor nutcrackers oriented accurately in initial tests of this sort, though some nutcrackers eventually learned to do so. Moreover, people behaved similarly if, like nutcrackers, they had to learn for themselves that the goal was at a constant location in the room. Rather than developing a representation of the goal within the room, subjects of all species tested relied much more than they should have on local cues such as the vector between the edge of the enclosure and the goal. In larger-scale space too, people do not do a good job of relating their orientation within an enclosed area such as a room to that within the surrounding environment (Wang and Brockmole 2003).

Some different results have come from another test of knitting together devised by Blaisdell and Cook (2004) for pigeons. As in second-order conditioning in learning of temporal relations (Section 4.4.3), the animal is first exposed to a relationship between two neutral stimuli, simultaneously presented landmarks rather than successively presented tones, lights, or the like. Then it learns to locate food with respect to one of those landmarks, and finally, it is tested with the other. For example, suppose in the first phase A is west of B, and in the second, food is south of A. Knitting together these two experiences would lead the animal to search southwest of B in the test. Generalizing from A to B, a possible alternative strategy, would be expressed as searching directly south of B. Pigeons behave as if connecting the two experiences, whether the landmarks are presented in an open field (Blaisdell and Cook 2004) or on a touchscreen (Sawa, Leising, and Blaisdell 2005). However, in a video simulation of the open field task people at first show generalization between the A and B landmarks (as indeed the pigeons did in the actual open field), but gradually transfer their searching to the site specified by integration (Sturz, Bodily, and Katz 2006). This pattern may reflect learning from initial nonreinforced searches in the test rather than a mapping-like process. However, rats tested in a slightly different way do seem to knit together separately experienced items of landmark information (Chamizo, Rodrigo, and Mackintosh 2006). Rats were trained to find the hidden platform in a water tank in intermixed trials with two sets of three landmarks having one member in common (e.g., landmarks A, B, C and C, D, E). Unlike control rats trained similarly but with nonoverlapping sets of landmarks, those for which the sets shared a member preferred the part of the tank with the platform when tested with a novel combination of landmarks (e.g., A, B, E). The variety of results here indicates that much remains to be done to understand the extent to which animals knit together separately experienced spatial relationships into an overall "map."

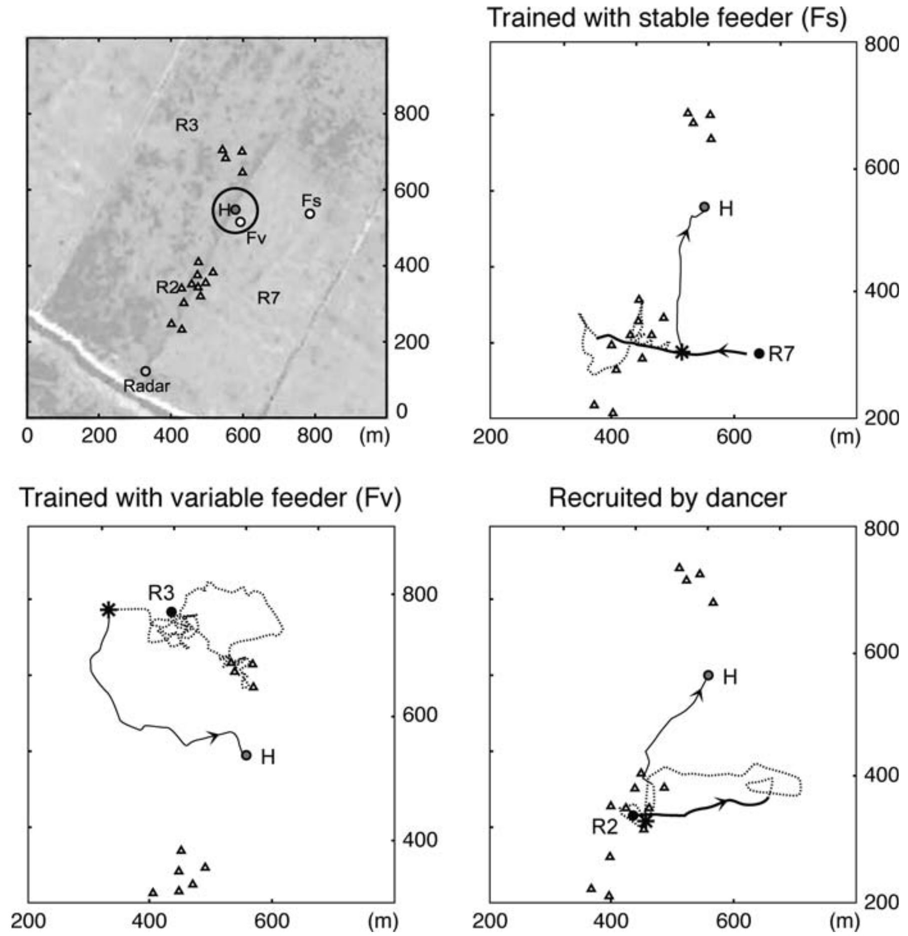
Australian desert ants (*Melophorus bagoti*), however, fail entirely and in a surprising way to knit together information obtained in different parts of a journey. The ants are an instructive corrective to anthropomorphism, a reminder of how almost unimaginably strange ways of navigating can be perfectly effective in the natural conditions in which they are normally used. Unlike the Tunisian desert ants we met in Section 8.1, the Australian species live among grass tussocks that provide landmarks, which the ants evidently use along with global path integration somewhat as illustrated in Figure 8.12. By means of a system of barriers, Wehner and colleagues

(Wehner et al. 2006) forced ants to adopt different outward and homeward paths across such terrain to a constant food source. Within a few trips, each ant developed an idiosyncratic round trip route. Having thus shown that they knew the way to the food and home again, the ants were picked up while on the way home with a biscuit crumb and placed down partway along the outward path. What they did then depended on how close to home they were when picked up, but in no case did ants behave as if recognizing where they were on the outward path by either heading back along it or taking a shortcut home. Rather, ants that were still some way from home ran in the direction of the global vector that would have led them home from where they were collected. Ants whose global homing vector was at zero because they were caught just before entering the nest behaved as if lost, searching in circles until they hit the homeward route. To quote the authors' summary, "familiar landmarks are not decoupled from the context within which they have been acquired and are not knitted together in a more general and potentially map-like way. They instruct the ants what to do rather than provide them with map-like information about their position in space" (Wehner. et al. 2006, 75).

Cognitive maps in bees revisited

Dyer's bees tested in the quarry behaved similarly to the ants deprived of familiar landmarks by orienting along the vector that would have taken them to their destination from their original starting point. Indeed, for bees commuting between the hive and a customary feeding site, running off a fixed vector back and forth is very efficient. But what happens when vector information tells displaced bees they should already have arrived? It turns out that at about this point, some maplike knowledge takes over. Menzel and his colleagues (2005) captured experienced bees as they were about to start home from a feeder and quickly fitted them with harmonic radar antennas before releasing them within about 500 meters of the hive but at a different direction from it. The records of displaced bees' entire homeward paths so obtained show that bees trained with a feeder in a stable location flew directly away from the release site in the direction they would have taken to return to the hive (Figure 8.23). Bees that had attended the dance (see Chapter 14) of a bee returning from the stable feeder behaved similarly. After perhaps a few hundred meters this straight flight gave way to a circuitous searching flight, which was then followed by a second phase of straight flight, headed directly to the hive or the feeder. Circling appeared to allow the bees to recognize some features of the landscape from which they knew the homeward vector. Bees that had been trained to a feeder at varying locations immediately began searching flights.

As Cheng (2006) points out, these findings need not mean that bees have an exhaustive knowledge of places around the hive because a bee finding itself with a view similar to that from two familiar locations would presumably still wind up at its goal by generalizing and averaging the resulting vectors. Nevertheless, as R. Menzel et al. (2005) conclude, the bees' behavior implies that they have maplike knowledge in the form of learned vectors from a variety of familiar locations to the hive and/or the feeder, that is, a vector map. That is to say, the bees have evidently learned vectors linking certain known locations and can compute routes home from them, but they do not necessarily have a comprehensive metric map of their territory. Moreover, they apparently do not reverse the process, in that when told a vector along which to head from the hive in the form of another bee's dance, they do not behave as if


Trained with stable feeder (Fs)

Trained with variable feeder (Fv)

Recruited by dancer

Figure 8.23. Top left: overhead view of the landscape in which bees were tested for maplike knowledge, showing location of the hive (H), the feeder for the stable feeder group (F_S), the tent landmarks (triangles), and several of the experimental release points (R). Remaining panels show paths of one bee from each of the three training groups. Dark lines signify a straight initial flight from the release point. After R. Menzel et al. (2005) with permission.

imagining the location danced about but rather fly to that location even if it is an implausible place for food (see Chapter 14; Wray et al. 2008).

8.4.3 Vertebrates mapping their home ranges

As we have seen, cognitive mapping was originally tested with rats in the laboratory with little or no reference to what the animals might be doing in nature. Indeed, because wild rats are nocturnal and tend to travel along habitual routes and paths (Chitty and Southern 1954), it is not clear what role the visual orientation commonly tested in laboratory rats might have in nature. Ants and bees are more appropriate subjects because their experience can be manipulated in the field and their behavior observed on spatial scales representative of normal foraging trips. As yet no vertebrate has lent itself to such a rich body of work, but a sample of studies of homing pigeons and mammals indicates possibilities for future investigations.

Maps and routes in homing pigeons

Given that people have exploited pigeons' homing ability for thousands of years (Wiltschko and Wiltschko 2003), how pigeons find their way home is still surprisingly controversial (Wallraff 2005). The prevailing view is that they use a "map and compass" mechanism, that is, a way to recognize where they are combined with knowledge of which compass direction to head to reach the home loft. Experiments with clock-shifted birds have established that the directional information may be provided by the sun compass (Box 8.2), but other information is important too. When pigeons start home from unfamiliar locations far from their loft, their "map" is in effect a sense of position relative to home based on olfactory, magnetic, or possibly auditory cues (see Wallraff 2005). Remarkable though it is, this is not a cognitive map in the usual sense. And when pigeons home repeatedly from the same site 7 to 10 kilometers from home, they may not refer to a maplike representation either. Rather, data from tiny GPS trackers carried by flying pigeons show that they may develop stereotyped, idiosyncratic, routes. Somewhat like the Australian desert ants or honeybees, when they are released off their usual routes, they first head not toward home but toward the habitual homeward route (Biro, Meade, and Guilford 2004; Meade, Biro, and Guilford 2006). Under the conditions of this study in the richly detailed countryside around Oxford, the pigeons' usual route seems to be encoded as a series of landmarks or views of the landscape. However, the distances involved and other factors apparently influence whether pigeons develop such stereotyped routes (Wiltschko, Schiffner, and Siegmund 2007). In addition, evidence that clock-shifted birds follow their sun compass rather than a familiar route (Wiltschko, Siegmund, and Stapput 2005) indicates that much remains to be understood about the way in which pigeons integrate different sources of navigational information. When orienting in a familiar landscape, they likely use many more kinds of cues than can ants or bees, relying on different ones according to the circumstances (Keeton 1974; Wallraff 2005).

Meerkats finding boltholes

Meerkats (*Suricata suricatta*) are a species of social mongoose found in the southern African semi-desert. We meet them again in discussing social learning and communication (Chapters 13 and 14), reflecting the fact that one South African population has been intensively studied for many years (cf. Ross-Gillespie and Griffin 2007). Meerkats are primate-like in that they form stable social groups with overlapping generations living in a more or less permanent territory. Animals with such a social system obviously have ample opportunity acquire detailed knowledge about what is where and how to get there. Scattered through its 2–4 square kilometer territory, each group has two or more burrow systems for sleeping and raising young, but they also have numerous boltholes into which they can run for safety when threatened by a predator. By observing what meerkats did in response to naturally occurring and recorded meerkat alarm calls, Manser and Bell (2004) showed that the animals know the locations of boltholes. For example, they headed for the nearest bolthole 83% of the time, whether or not it happened to be one they had recently passed while foraging. Meerkats ignored new, human-made, boltholes, even when these were closest to them when an alarm call was heard. In constrast, if the nearest bolthole was one of their own that the experimenters had covered over with a car mat and sand, the meerkats ran to it and tried to get in. Thus their orientation is based on memory, not visual or olfactory cues from an open bolthole. Since a group may have hundreds of boltholes, these findings suggest that the meerkats have extensive and detailed spatial knowledge of their locations. Perhaps this is not surprising, given that they spend many hours each day moving through the territory digging for invertebrate prey and watching for predators. Exactly how they know the positions of nearby boltholes remains to be determined. Columbian ground squirrels (*Spermophilus columbianus),* another small burrowing mammal of comparatively open spaces, locate escape burrows primarily using global cues from the distal panorama of trees, mountaintops, and the like (Vlasek 2006).

In a further test of meerkats' spatial knowledge, on six occasions Manser (personal communication) captured an adult meerkat foraging with its group and released it about a kilometer away at one of the sleeping burrows within the group's territory. The animals traveled quite directly back to the location where they had been captured, arriving within 40 minutes on average. If the group had already moved on, the lone meerkat began looking around, sniffing the ground, and engaging in similar behaviors indicative of searching. The animals were not obviously using vocal or olfactory cues to find the place where they had been removed from the group, but apparently relying on visual recognition of local or global aspects of the landscape.

Monkeys mapping their home ranges

Like the meerkats, apes and monkeys seem likely to possess large-scale integrated representations of space. Field studies of monkeys and apes that involve following habituated groups on a daily basis have provided an abundance of information about the spatial and temporal distributions of the animals' food and how the animals travel between sleeping sites, water holes, fruiting trees, and other resources (Boinski and Garber 2000; Noser and Byrne 2007). The cognitive demands of tracking temporary and spatially dispersed food sources have been proposed to explain differences in relative brain size among primates, with the fruit-eaters supposedly needing larger brains than leaf-eaters (Chapter 12). Numerous field experiments have shown that various monkey species can learn the locations of artificially provided foods and travel among them in an efficient way (e.g., Janson 1998; Garber 2000). One clever study suggests that Japanese macaques (*Macaca fuscata*) remember the locations of trees with a favorite fruit from year to year. C. Menzel (1991) placed akebi fruit, chocolate, or nothing beside a troop's foraging route at a time of year when akebi fruit were not naturally ripe. Monkeys that discovered akebi often left the troop's foraging route and began looking up into akebi trees, whereas those that found chocolate searched the ground nearby.

Observations of unmanipulated animals are necessary for showing how such learning influences their daily travels. These are often very suggestive but must be interpreted with care (Janson 2000; Janson and Byrne 2007). Mapping where a troop of monkeys goes between leaving its sleeping site in the morning and returning in the evening may suggest the animals are planning their routes, but just as with examples of travel among multiple sites in a smaller space, planning ahead has to be distinguished from moving to the next nearest resource on the basis of locally perceptible cues. For example, to decide whether memory for a fruiting tree's location is being used, it is necessary to know the distance from which it can be detected directly, and that differs for forest and savannah species and with the thickness of vegetation across the year. The animals' nutritional needs relative to different available foods may help explain the sequence in which sites with those foods are visited. Constraints on travel such as needing to arrive at a safe sleeping site by nightfall may need to be taken into account. Noser and Byrne (2007) provide one example of attempting to deal with all these factors. Observed routes can be compared to those predicted on various models of random search (see Janson and Byrne 2007). And ideally, opportunistic observations can help to reveal how the animals' travels reflect what they know. For example, if a predator is encountered at a habitual waterhole, does the troop use another one the next day? In a similar way, the nature and rate of change in travel patterns with the seasons may indicate whether the animals are planning routes with certain goals in mind. For instance, visiting patterns and speed of approach indicate that mangabeys keep track of whether trees are already finished fruiting or are about to produce ripe fruit (Janmaat, Byrne, and Zuberbühler 2006). Such questions have been attracting increasing interest at the same time as they are being addressed in more sophisticated ways. One possibility (Janson and Byrne 2007) is that some primates' spatial knowledge encodes important locations and the routes or vectors between them, but without being a complete Euclidean survey map. Although it would likely represent more and varied types of sites than the vector map of the honeybees, it could be similar in kind.

8.4.4 But do people have cognitive maps?

Research on spatial cognition in human adults and children is a large area in its own right and can be given only a brief mention here (for an introduction see Newcombe and Huttenlocher 2000). As indicated by the scattered mentions of findings with people, much contemporary work in this area is closely integrated with that on other species, especially in looking at spatial behavior in terms of a number of distinct subprocesses and in failing to find evidence for overall cognitive maps. Nowhere is this more evident than in a prominent opinion piece titled "Human spatial representation: Insights from animals" (Wang and Spelke 2002). Wang and Spelke proposed that rather than depending on an enduring allocentric map, much human spatial behavior depends on momentary egocentric representations, specifically dead reckoning, orienting by the geometry of surrounding space, and viewpoint-dependent matching of remembered to current views of the environment. Evidence for each of these processes comes from animal data like that reviewed throughout this chapter and from analogous experiments with people. In one key example, people viewed a room with a few objects in it and were then blindfolded, disoriented, and asked to point to the objects and the corners of the room. Errors in pointing indicated that the objects had not been integrated either into a map of the room as a whole or into a single configuration (Wang and Spelke 2000). Evidence that recognition of a familiar scene takes longer from a novel viewpoint supports the suggestion that encoding is viewpoint-dependent. However, more recent research (Burgess 2006) indicates that human spatial representation has both egocentric and allocentric components, which exist in parallel. In experiments like those just summarized, greater experience, a larger environment, and other factors make allocentric representations more evident. This approach is clearly much in the spirit of other research emphasized in the present chapter in dissecting spatial cognition into distinct parallel but interacting mechanisms and eschewing discussion of overall maps. Whether two systems defined in terms of function, egocentric and allocentric, will provide a useful way forward remains to be seen.

8.4.5 Conclusions

The cognitive map has been seducing investigators for over 60 years, but perhaps it is no more than a metaphor based on human introspection. Just as with theory of mind and other hypothetical mechanisms discussed later in this book, attributing cognitive mapping to an animal may be an unwarranted exercise of anthropomorphism, and one that is not even very useful in explaining human behavior. Translating such an intuitively appealing explanation of apparently intelligent behavior into testable implications in a way that researchers agree on is never easy. When the results of behavioral tests cause theorists to revise ambiguous and slippery concepts, agreement can become almost impossible. In the case of cognitive mapping, there is little if any unambiguous evidence that any creature gets around using a representation that corresponds to an overall metric survey map of its environment. The exceptional cases in which animals satisfy one or another classic criterion for mapping-like behavior by taking novel short cuts in the absence of direct cues from the goal (Singer, Abroms, and Zentall 2006; W. Roberts, Cruz, and Tremblay 2007) or finding their way home when displaced (R. Menzel. et al. 2005) are better explained by reference to what cues the animals are actually using, how they are using them, and how they come to do so than to the ill-defined notion of a cognitive map.

8.5 Summary

The study of spatial orientation is a very active area using a wide variety of species and approaches from fieldwork to neuroscience (Box 8.4). Among areas of research in comparative cognition it is exemplary, perhaps unique, in the way in which data and theorizing have been integrated across species and approaches as for example in the book edited by Jeffery (2003). The richest bodies of data come from three very different groups of animals: small nocturnal rodents (rats and hamsters), diurnal, central-place foraging insects (bees, wasps, and ants), and birds that orient over tens to hundreds of kilometers (homing pigeons and migratory species). The ways in which these animals perceive the world (consider for instance the very different visual systems of rats, pigeons, and bees) and the cues relevant for orientation in their natural environments differ enormously, yet some orientation mechanisms such as landmark learning or path integration and their interactions have been analyzed in a way that cuts across phyla. To some extent, this integrative approach has resulted in a theoretical orientation based on ideas from human psychology being replaced by one rooted in data from nonhuman animals.

Box 8.4 Space in the Brain

The study of what parts of the brain, particularly in mammals, help to control spatial behavior and how they do so is a vast area of contemporary behavioral neuroscience. The fact that the hippocampus is important for spatial memory in both mammals and birds has already been alluded to in Chapters 2 and 7, but in itself this does not tell us much about how brains actually represent space. Until recently the primary relevant information consisted of evidence for *place cells* in the rat hippocampus, single cells that fire when the rat is in a particular location within a laboratory enclosure. However, although the properties of place cells have been studied in some depth, one property seemingly essential for coding space is apparently lacking, topographic organization. That is, cells close together in the hippocampus do not necessarily fire to places close together in space. Moreover, the same cell may have a place field (i.e., area in which it is active) in more than one enclosure (cf. Jeffery 2003).

The last few years have seen major advances in understanding how space is actually coded in the brain (see McNaughton et al. 2006). A major discovery is cells in the entorhinal cortex, *grid cells,* that map space in a periodic pattern whose spatial scale increases in an orderly way across layers of the medial entorhinal cortex. Combined with signals from cells sensitive to the animal's head direction and perhaps self-motion cues, these have the potential to code changes in an animal's position. Just as a unique time could in principle be coded by simultaneously reading the states of multiple oscillators with different frequencies (Section 9.3.2), so a location in space can be represented in terms of overlapping tessellations of tiles ranging from quite small to nearly the size of the space. New paradigms that require rats to navigate by dead reckoning have been used to probe the function of grid cells. In addition, hippocampal place cell recordings from rats moving over much longer distances than in traditional studies (e.g., 18 meters) show that the size of place fields increases across the hippocampus, perhaps providing a means to encode both details of space and general spatial context (see Hasselmo 2008).

This chapter began with descriptions of the wide range of mechanisms animals use for getting around. By itself, each of them has advantages and disadvantages. Dead reckoning is most useful for short journeys back and forth to a central place, especially in an environment with relatively few landmarks, as in the dark or on the desert. Other ways of getting back and forth to a starting place include route learning both in the sense of a memorized sequence of motor patterns (response learning) and in the sense of a sequence of responses to landmarks. Dead reckoning and route learning in either sense leave the animal lost if it is displaced too far off its usual route. However, stimulus generalization between familiar and unfamiliar views of the environment gives route learning some flexibility.

The varieties of spatial information—from landmarks, beacons, dead reckoning, environmental shape—are processed in different cognitive modules which take different kinds of input and output decisions about what distance and/or direction to move relative to different kinds of cues. This raises the question of how the outputs of different spatial modules are combined during the acquisition and use of spatial information. Are different kinds of information processed in parallel, do they compete for learning as in conditioning, or are they integrated in some other way? When are modules used in a hierarchical manner, and why? When spatial cues have acquired their significance, do they compete for control or are their outputs averaged? When does each kind of combination rule operate? For instance, does the system that has been more reliable during evolution or individual experience or that evolved earlier take precedence? A great deal of attention has been devoted to the question of whether any animal integrates different sources of spatial information into a unified allocentric representation of distances and directions, a cognitive map. This question turns out to be difficult to answer, partly because cognitive maps can mean different things to different people. Focusing on the specific cues available to animals and how they are used in specific situations provides better understanding of how animals get around than attempting to prove or disprove use of a cognitive map.

Further reading

Useful recent reviews of most aspects of spatial cognition can be found in the books edited by Jeffery (2003) and Wasserman and Zentall (2006b) and the online "cyberbook" edited by Brown and Cook (2006). Boinski and Garber's (2000) *On the Move* emphasizes field studies of animal movement patterns; the July 2007, special issue of *Animal Cognition* discusses numerous examples from primates. Newcombe and Huttenlocher's (2000) book is an excellent introduction to the development of spatial cognition in children very much in the same spirit as this chapter. The book by Wallraff (2005), the review by Bingman and Cheng (2005), and the special section of the August 11, 2006, issue of *Science* provide more information on homing and migration.

Some of the classics in the area are still well worth reading. These include the first six chapters of Gallistel (1990), with all aspects of animal spatial cognition discussed in the context of human navigation. The first two chapters of O'Keefe and Nadel's (1978) book are an excellent introduction to philosophical and psychological notions about space. A facsimile of this entire book is available free at http://www.cognitivemap.net. For a discussion of exploration, Berlyne (1960) still contains a lot of wisdom and a summary of much psychological and ethological literature.

9
Timing

As sunset gives way to dusk, bats and nighthawks appear, swooping and gliding over city rooftops or above surfaces of lakes, catching insects. Like most other living things, these animals have an internal rhythm, a biological clock with a period of about 24 hours that allows them to become active at the same time each day. Some of the most impressive evidence for such a clock is the nightly appearance of thousands of South American oilbirds pouring out from their roosts deep in caves where no sunlight reaches.

Clocks that time intervals much less than 24 hours are evident in classical and instrumental conditioning. Pavlov (1927) described the first examples. For instance, a dog trained with a three-minute whistle predicting weak acid to its mouth salivated most during the last minute of the whistle. This phenomenon, which Pavlov called *inhibition of delay,* suggests that the dog was timing the signal. Contemporary research on how animals time intervals seconds to minutes long includes some of the most elegant experiments and quantitative models in the study of animal cognition. It is worth knowing about for that reason alone. Timing is also worth knowing about for functional reasons. Information about how animals time events will come in handy in Chapter 11, on foraging and instrumental behavior. For instance, models of foraging suggest that animals need to be sensitive to rates of occurrence. Mathematically, rate is number divided by time, so this idea implies that we need to know how animals time and count (Chapter 10) to understand foraging.

9.1 Circadian rhythms

The regular alternation of day and night is perhaps the most predictable event on Earth. Therefore it is not surprising that nearly every organism that has been studied, including plants, bacteria, and human beings, has an internal model of this daily rhythm. This internal model is evident in a daily cycle of activity and/or physiological state which persists even when organisms are kept in unchanging light or darkness. Circadian rhythms are not usually regarded as part of cognition, but they appear in this book for three reasons. First, the way in which circadian rhythms are synchronized with (or *entrained to*) local day and night is an instructive example of behavioral plasticity in response to experience. Biological rhythms illustrate beautifully the general principle that animals have evolved implicit internal representations of important aspects of the world, representations programmed to be modified in adaptive ways by events that are functionally relevant in nature (Shepard 1984, 1994). Second, in a kind of learning that is important in the wild, animals learn about events that recur on a daily basis, linking them to the state of their circadian clock. Finally, understanding something about timing daily events is necessary for understanding proposals that timing intervals of seconds to minutes involves the same mechanism.

9.1.1 Entrainment: Synchronizing endogenous cycles with environmental cycles

Some animals, like most of us, wake in the morning and sleep at night. Others, like bats and moths, do the reverse. Still other species are most active at dawn and dusk. Although casual observation in nature suggests that daily rhythms of activity are driven by cues from the environment, most daily rhythms run independently of the environment but need continual environmental input to remain synchronized with day and night. The very earliest studies of biological rhythms revealed that daily rhythms of activity and other physiological variables persist, often indefinitely, when animals are isolated from the influence of local day and night. The persistent rhythm cannot be produced by some unknown signals from the earth's rotation reaching into laboratory rooms because these *free-running* rhythms are generally slightly more or less than 24 hours long. Thus, for example, after awhile animals in the laboratory will be active when their conspecifics outdoors are asleep. Because the *endogenous* (i.e., self-generated) daily rhythm is not exactly 24 hours long, researchers refer to *circadian* rhythms, that is, rhythms of approximately (*circa*) a day. Figures 9.1 and 9.2 show examples.

The process by which the underlying rhythm-generator or *pacemaker* is synchronized with environmental signals is referred to as *entrainment*. The signal that entrains the rhythm is referred to as an *entraining agent* or *zeitgeber* (literally "time-giver" in German). The most-studied zeitgeber is light, but other stimuli can also function as entraining agents (Mrosovsky et al. 1989). Our examples are almost all from activity rhythms because these are easily measured in the laboratory and have featured in many studies, but most physiological functions exhibit a daily cycle; it is difficult to find one that does not. The propensity to be entrained is an adaptive feature of the circadian system that adjusts behavior to the local environment. However, the behavioral and physiological variables controlled by the underlying circadian pacemaker can also be influenced in ways other than by entrainment. For example, during a total eclipse of the sun, birds stop singing and sit still, as if dusk were falling. Conversely, a diurnal rodent asleep in its burrow is stimulated to activity if a predator breaks in on it. Such transient changes *mask* underlying rhythms.

Several well-defined criteria characterize entrainment (Dunlap, Loros, and Decoursey 2003): *(1)* The putative entraining agent must act in the absence of other cues. *(2)* It must act to adjust the period of the animal's free-running rhythm to the period of the signal. The unlikely hypothetical case in which a signal repeated every 19 hours caused an animal to become active every 24 hours would not be entrainment because the periodicity of the behavior would not match the periodicity of the signal. *(3)* The entrained rhythm must adopt a stable phase relationship with the imposed cue. For example, if a group of animals is isolated in constant light or constant darkness, the free-running rhythms of different individuals will eventually be out of phase with one another, reflecting individual differences in free-running period. Yet if they are all now exposed to the same light-dark cycle, before very long their activity rhythms will be synchronized with the environment and,

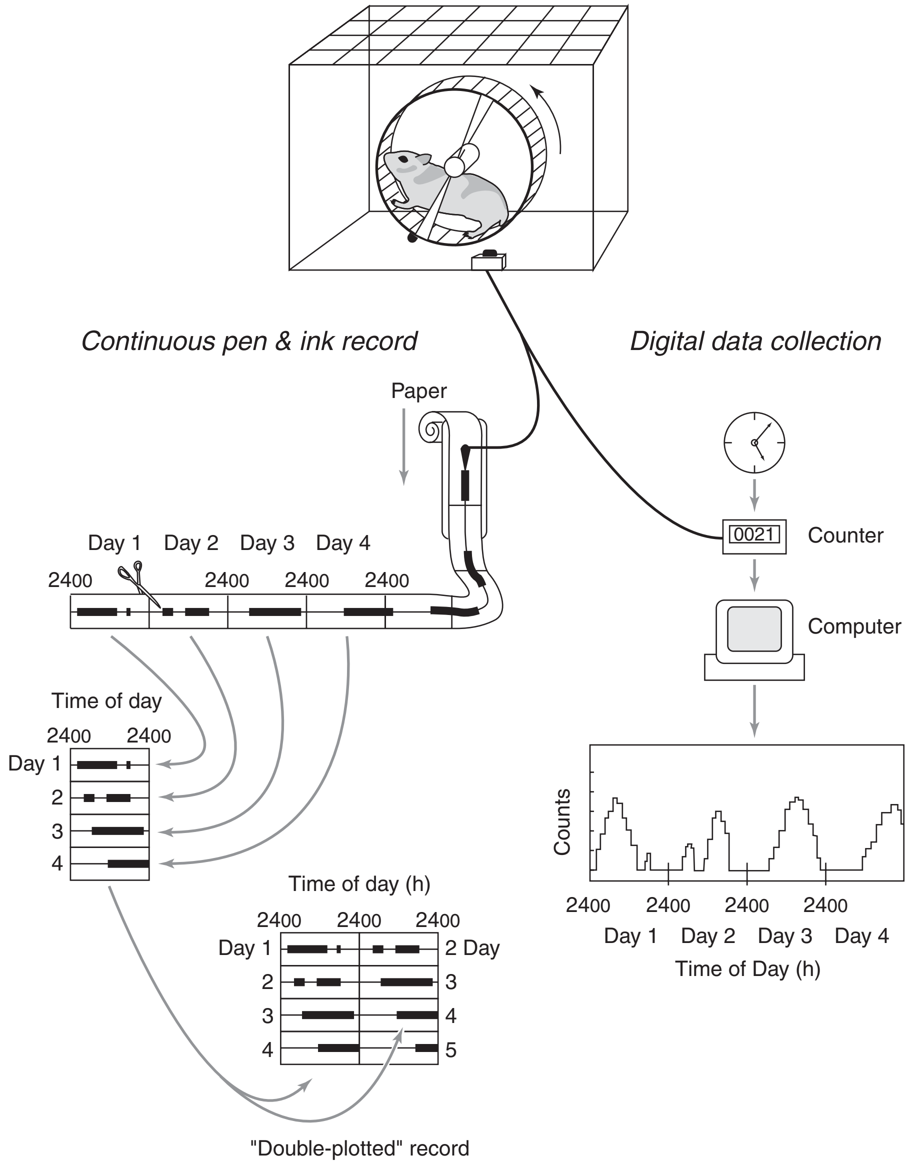


Figure 9.1. Setups for recording rhythms of locomotor activity in hamsters and typical data. (Golden hamsters are used in much contemporary research on mammalian rhythms because they have exceptionally clear and reliable rhythms of running wheel activity.) In the traditional method (left), each revolution of the running wheel results in a pen mark on a continuously running roll of paper. When the records of successive days are mounted one under the other, as at the lower left, regularities in the daily pattern of activity can easily be picked out by eye. This is even easier when each day is "double plotted," as at the bottom. Using a computer to record the activity, as is often done nowadays, may facilitate detailed quantitative analyses. Redrawn from Moore-Ede, Sulzman, and Fuller (1982) with permission.

incidentally, with one another. The original phase relationship of the pacemaker with the entraining agent does not influence the final, species-specific, relationship. *(4)* Entrainment can be distinguished from direct driving of the rhythm (i.e., masking)

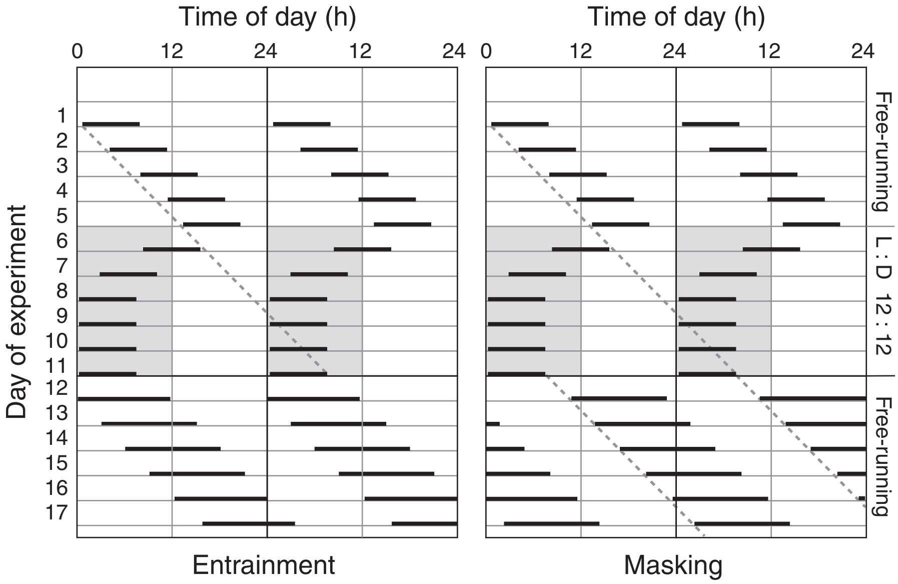


Figure 9.2. The contrast between entrainment and masking. A free running activity rhythm (in this case, one with a period slightly greater than 24 hours, as indicated by its drift to the right) is synchronized by imposition of a 12-hour light—12-hour dark schedule (L:D 12:12; gray rectangles represent the dark period). When the synchronizing cue is removed, the animal on the left shows that it has been entrained; the other's activity returns to where it would have been without the cue, indicating that the underlying rhythm had simply been masked by the L:D cycle.

by putting the animals back into constant conditions and observing the relationship between the phase of the free running rhythm and the phase of the just-removed environmental cycle (Figure 9.2). If the animals in our example are truly entrained, then their activity rhythms will all start their free-running drift in the same place. For example, if laboratory "dawn" and the onset of activity had been at local 10 AM, the animals will still become active about 10 AM on the first day with constant light. However, if the laboratory light cycle is simply masking the effects of the circadian pacemaker, each animal may become active at a different time when constant conditions are instituted. In masking, the time of activity is predicted by extrapolating from the drift in the free-running rhythm before the environmental cue was imposed (Figure 9.2).

Entrainment is a kind of behavioral plasticity in which the animal's internal model of the cycle of day and night is brought into register with true day and night. Like many other kinds of preprogrammed adaptive behavioral plasticity, entrainment of the 24-hour activity rhythm is most sensitive to modification by conditions close to those found in nature. Circadian rhythms can be entrained only to periods of about 24 hours. "About 24 hours" means different things for different species and situations, but a range of three or four hours around 24 hours is typical. Thus, it might be possible to entrain activity to 22- or 26-hour days (i.e., a period of light plus a period of darkness every 22 or 26 hours), but unlikely that the rhythm could be entrained to 19 or 29 hour days.

The fact that a free-running rhythm can be brought into a predictable relationship with a zeitgeber means that a cycle of changing sensitivity to the zeitgeber underlies the measured behavioral or physiological rhythm. This sensitivity can be revealed by

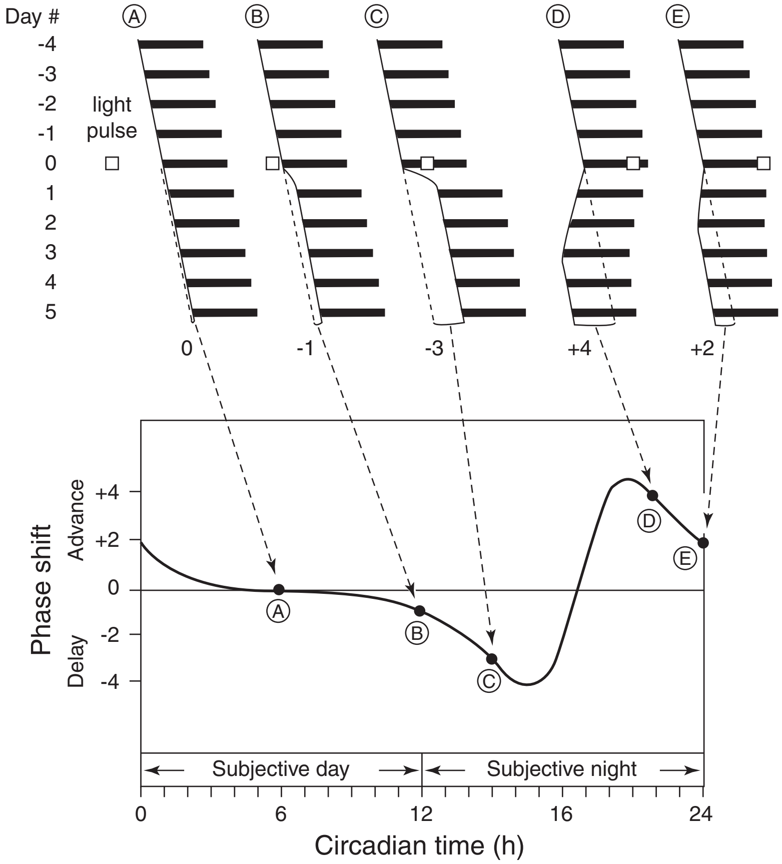


Figure 9.3. A phase-response curve and how it was derived. Data are from five experiments with a nocturnal species. In each, a brief pulse of light is presented at a different phase of the free-running rhythm and the effect on activity in the next few days is measured as number of hours' advance or delay in activity. Redrawn from Moore-Ede, Sulzman, and Fuller (1982) with permission.

experiments in which a single pulse of light 10 or 15 minutes long is presented to animals free-running in constant darkness. The effects of a few minutes of light on one occasion are evident in the ensuing few days, in which the activity rhythm first shifts and then runs freely again. Figure 9.3 shows an example for a nocturnal animal like a golden hamster. In a regular 24-hour cycle of light and dark, the animal would become active at the onset of darkness. When the rhythm is free running, the period of activity reveals this noctural animal's *subjective night; subjective day* is the period of prolonged inactivity. (For a diurnal animal the terms reverse: subjective day is the active period.) In this typical example, a pulse of light early in the subjective night causes the animal to become active later the next day, that is, the phase of the rhythm has been delayed relative to the external 24-hour cycle. Conversely, a pulse of light toward the end of the subjective night advances the rhythm: the animal becomes active earlier the next day. Somewhere toward the middle of subjective night, the effect of a light pulse switches from delaying to advancing. Light has little or no effect in the middle of subjective day. Hamsters' activity rhythms can also be entrained by social stimulation like the regular arrival of a mate or rival or by activity in a novel environment. Such zeitgebers have a characteristic pattern of effects different from those of light (Mrosovsky. et al. 1989).

The fact that the circadian rhythm is most sensitive to light near the beginning and end of subjective night means that in nature dawn and dusk are constantly pushing and pulling animals' endogenous circadian rhythm into synchrony with day and night. In the laboratory, synchrony can be produced by exposing animals to *skeleton photoperiods,* that is, a pulse of light at the beginning of laboratory "day" and another one at the end. This mimics the regime that a nocturnal cave- or burrow-dweller might expose itself to naturally. If it ventures out too early in the evening, its activity will begin later the next day (i.e., its rhythm will be delayed), whereas if it stays active too long, the pulse of light at dawn will advance its activity, causing it to rise earlier the next night. This suggests that an animal that stays in its den for many days on end may become desynchronized with the external day and night (i.e., its rhythm will free run). This is exactly what happens to beavers that stay in their lodges and under the snow-covered ice throughout the Canadian winter (Bovet and Oertli 1974).

The direction and amount of shift in the free-running rhythm produced by a single pulse of light are summarized in a *phase response curve,* a plot of the response of the rhythm to a constant signal as a function of the rhythm's phase when the signal was applied. Figure 9.3 shows an example and how it was derived. A phase response curve (PRC) is analogous to the function relating learning to the CS-US interval or the number of conditioning trials (Chapter 4) in that both describe the effect of an environmental event as a function of systematic variation in its features. Learning is usually thought of as generating new knowledge and behavior whereas entrainment brings a preexisiting cycle into register with a cycle in the environment. However, as we have seen in Chapter 4, conditioning can be seen as bringing a preorganized sequence of behavior, or a behavior system, under the control of certain kinds of environmental events (Timberlake 1994). This provocative analogy summarizes the notion that conditioning does not create the behavior expressive of conditioning any more than entrainment creates the behaviors that change on a circadian cycle. But it is no more than an analogy: entrainment and associative learning otherwise have very different properties.

9.1.2 Effects of regular meal times

A major function of the circadian system is to allow each behavior to be performed at the most appropriate times of day. The most-studied example is feeding. Hummingbirds or bees may find their favorite flowers open only in the morning; kestrels find their rodent prey out of their burrows at some times and not others (Rijnsdorp, Daan, and Dijkstra 1981). Many animals adjust their activities to such periodic feeding opportunities, but how do they do it? There are three possibilities. One is that the circadian oscillator that can be entrained by light is also entrained by regular feeding. A second possibility is that activity in anticipation of regular feedings represents the output of a second endogenous oscillator that is entrained by food (i.e., a food-entrainable, as distinct from a light-entrainable, oscillator). Third, the animal may simply learn at what time of day, that is, at what phase of its circadian clock, to expect food. There is evidence for each of these, although it is not yet clear how the species and/or situation determines which one(s) will be seen.

A landmark study in this area was one in which rats in running wheels were fed two one-hour meals a day, at 10 AM and 4 PM (Bolles and Moot 1973). The rats soon began to show a pattern of anticipatory running that began in the hour or so before

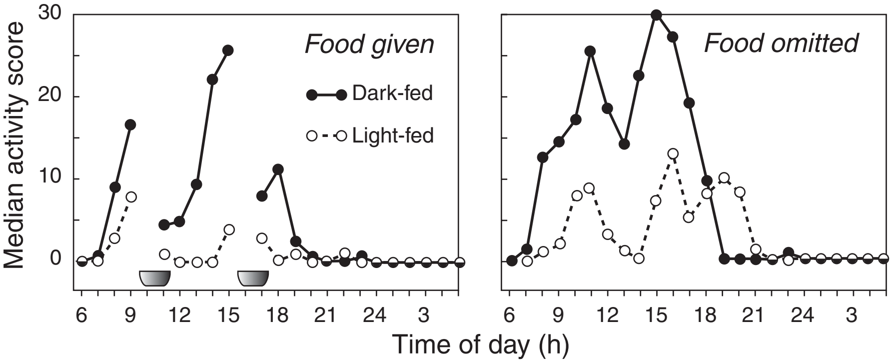


Figure 9.4. Running activity (wheel revolutions per hour) of rats fed twice a day, during the dark or the light phase of the light-dark cycle, and activity in a test with food omitted. Notice that both groups appear to anticipate the food. Redrawn from Bolles and Moot (1973) with permission.

each feeding and increased up to the time when food was given (Figure 9.4). Because hunger was presumably greater near 10 AM, after 17 hours of deprivation, than near 4 PM, the rats must have been using time of day as a conditional cue and not simply running more as they became hungrier. Moreover, when food was omitted on test days, running peaked around the usual time of feeding, then declined and increased again before the next usual mealtime. Thus the rats were apparently learning when their mealtimes were. It could be suggested instead that the two periods of running represent the output of two separate food-entrainable oscillators. However, this kind of interpretation becomes less plausible when there are more separate mealtimes to learn as in the first example of time-place learning in the next section.

The idea that feeding entrains a separate circadian oscillator rather than conditioning anticipation to a particular phase of the rhythm entrained by light is supported by observations that rats in constant darkness, that is, with free-running circadian rhythms, become most active just before feedings if the feedings are at a consistent time of day. The same conclusion is supported by neurobiological studies. Rats with lesions to the suprachiasmatic nucleus of the hypothalamus, which abolish circadian rhythms, still show activity that anticipates daily feedings (review in Mistlberger 1993). However, when they are required to bar press for food, rats do learn about interfood intervals of 17 or 30 hours (Crystal 2001), although they discriminate these intervals less well than those near 24 hours. The implications of this finding for theories of interval timing are discussed in Section 9.3.2.

The relative contributions of entrainment and learning about circadian phase to the effects of periodic feedings vary across species (Mistlberger 1993). Bees appear to have just one circadian oscillator, which can be entrained by food as well as light. Bees kept in constant light and offered sugar water once a day had their activity rhythm entrained to the time of feeding (Frisch and Aschoff 1987). Each experimental nest's daily bout of activity shifted progressively until it began around mealtime, that is, the phase of the rhythm and the zietgeber had a predictable relationship. Furthermore, when feedings stopped, each nest's activity free-ran from its new position in time, satisfying another criterion for entrainment. The few species that have been studied in depth also appear to differ in the number of different daily feeding times they can learn. Bees and birds may be able to learn more different times than rats (Mistlberger 1993).

The preceding brief review indicates that in some species and situations, regular feedings at one or more times of day entrain a distinct circadian oscillator while in others they linked by learning to the circadian rhythm entrained by light. Learning about time of day may take place because the internal 24-hour rhythm acts as a contextual stimulus with which other events like feeding or the arrival of a mate or predator are associated. On this view, learning that food occurs at noon is no different from learning that food occurs in a striped chamber or when a tone is on rather than off. Memories may be better retrieved at the time of day when they were originally formed than at other times, although, like other phenomena reviewed in this section, this "time-stamp" effect varies with species (McDonald. et al. 2002).

9.1.3 Daily time and place learning

A rat in a cage becoming active before the time of feeding is showing that it knows when food is coming. But in nature, food doesn't just drop into a rat's burrow. The animal has to know where to get food, so anticipatory activity may function to get animals to the right place on time. Indeed, one of the first examples of circadian rhythms ever studied was the predictable arrival of bees at the jam pots on a family's outdoor breakfast table (see Gallistel 1990). Because flowers may be producing nectar only at certain times of day, the ability to learn time and place is important to bees, hummingbirds, and other nectar feeders. Carnivores, too, may develop daily routines based on time-place associations. For example when Rijnsdorp, Daan, and Dijkstra (1981) regularly released mice in a field at a time when kestrels (*Falco tinnunculus*) were seldom seen there, the birds' visits to that field became more regular around the release time. Learning about time of day may also allow family members to coordinate their activities with one another. Young rabbits and hares meet their mother for nursing just once or twice a day (Gonzalez-Mariscal and Rosenblatt 1996). Ring dove parents share incubation: the male sits on the nest most of the day and the female the rest of the time (Silver 1990). Each member of the pair leaves off foraging and approaches the nest at a distinctive time of day.

In the prototypical laboratory demonstration of daily time and place learning (Biebach, Gordijn, and Krebs 1989), individual garden warblers (*Sylvia borin*) lived in a large cage which had a central area with four feeding compartments ("rooms") opening off it (Figure 9.5). During each three-hour segment of the daily 12-hour period of light, food was available in a different room. The bird had to start in the central chamber and move into one of the rooms to feed. If it chose the correct room for the current time, it found the door over the food bowl unlocked for a few seconds. After feeding, the bird could return to the central area and make a new choice. Once the birds were apportioning most of their visits appropriately, they had tests with food available in all four places throughout the day. The pattern of visits persisted, indicating that the warblers were not simply going back to the room where they had most recently been fed (Figure 9.5). A further test of whether the pattern of visits was associated with the circadian clock consisted of preventing birds from visiting any of the feeding rooms for one 3-hour period. When visits were permitted again, birds went most to the correct room for the time of day, not the room that would normally follow the one they had been visiting before the block (Krebs and Biebach 1989). Furthermore, when garden warblers or starlings that had learned a time-place pattern were placed in constant dim light with food always available in all four rooms, the pattern persisted for several days (Biebach, Falk, and Krebs 1991; Wenger, Biebach, and Krebs 1991).

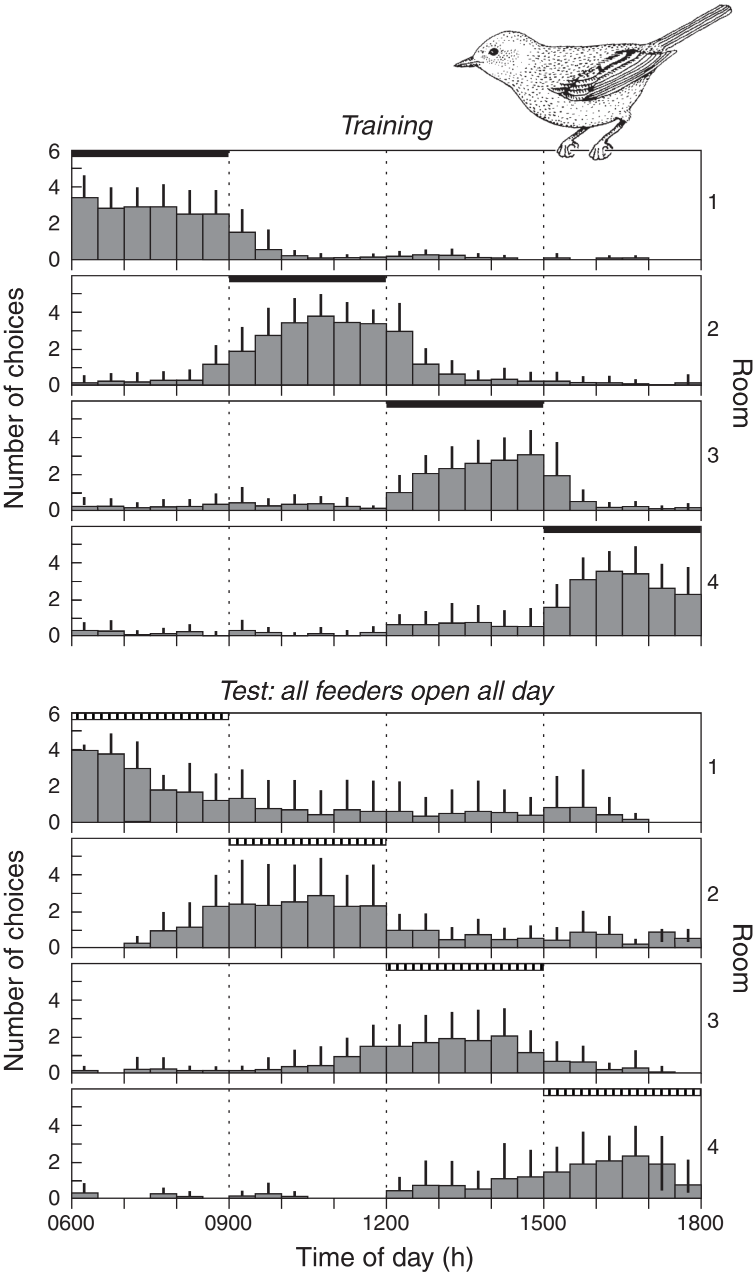


Figure 9.5. Time and place learning in garden warblers, illustrated by the number of entries to each room per half hour throughout the day. During training, food was available for three hours in each of rooms 1 to 4, in that order (dark bars). After Biebach, Gordijn, and Krebs (1989) with permission.

The garden warblers evidently used circadian phase to search primarily in the correct place at each time of day, but clearly this is not the only way to solve a daily time-place learning task. Consider, for example, a task with only two times and places such as has been used for rats, pigeons, and other species (C. Thorpe and Wilkie 2006). Animals might be put into an apparatus with two or more feeding locations at 9 AM and again at 3 PM with reinforcement at location A in the morning and location B in the afternoon. This discrimination could be based on interval timing, using the fact that the first session is, say, 3 hours after the lights come on in the home cage and the second session is 6 hours later. Alternatively, it could be based on *ordinal timing* (Carr and Wilkie 1997), that is, encoding sessions as first or second in the day. This seems more likely when the experimenter schedules feeding opportunities by taking the animal from its home cage and placing it in an apparatus for separate sessions than when the option to visit a possible feeding site is always available, as in nature or in the experiment with garden warblers. And of course ordinal, interval, and/or circadian timing could be combined, for instance using the interval from lights-on to the morning session and encoding the afternoon session ordinally, as "second."

The different behavioral implications of these three mechanisms are illustrated by a study in which rats learned a daily time-place task with three times and locations, A, B, and C (Pizzo and Crystal 2002). A was always correct in the morning and C in the afternoon, but the session in which B was correct was immediately after A for subgroup AB-C, and immediately before C for subgroup A-BC. Once the rats had learned to direct most of their choices to the correct location for each time of day, they were tested with session B moved either late (for subgroup AB-C) or early. If they had been basing their choices in session B on the fact that it was second in the day, behavior should not have been disrupted, but instead rats chose at chance in this test, more consistent with circadian timing. In a further test, the light-dark cycle in the rats' colony room was eliminated, along with other cues such as feeding during the sessions that could have been used for timing the intervals before and between daily sessions. Consistent with reliance on circadian timing, in this brief test the rats still tended to choose the correct site for each session, but consistent with some role for interval timing, they did not perform as well as when all the putative timing cues were present. A variety of other studies of this general type, primarily with rats and pigeons, have shown that daily time-place learning tasks may be solved in many ways, depending on factors such as the discriminability of the time intervals and other relevant cues (Thorpe and Wilkie 2006; Crystal 2006a). Originally, however, interest in daily time-place learning was stimulated by Gallistel's (1990) claim that animal memories consist of linked records of what, where, and when (in the sense of circadian time). It is now clear that animals can indeed base feeding decisions on circadian time and that under some conditions other cues are used as well. A recent example with bees related to episodic memory is the study by Pahl and colleagues (2007).

9.1.4 Summary

Circadian rhythms of activity and rest run freely in constant conditions. They are adjusted to the local environment by the process of entrainment, which has several distinct properties. To decide whether activity that anticipates a regular environmental event reflects entrainment, several questions need to be asked (Aschoff 1986). Is the effect described by a phase response curve, that is, does the possible entraining agent pull the free running rhythm into a predictable relationship with itself? Does the rhythm free run from its new phase when the entraining agent is removed? Does the effect of the putative entraining agent depend on its original relationship to the free running rhythm? For example, the effects of social stimuli on hamsters' subsequent activity depend on when in the circadian activity cycle they occur, indicating that they entrain the rhythm (Honrado and Mrosovsky 1991), whereas in the experiment in Figure 9.5 birds seem to associate each feeding place with the appropriate time of day. Learning about the times and places of food availability, encounters with predators, prey, or conspecifics, probably all play a role in organizing animals' daily routines. When memory for time and place develops in a single trial (e.g., Pahl et al. 2007) it might qualify as episodic-like (Chapter 7).

9.2 Interval timing: Data

In circadian timing, an endogenous oscillator that runs freely in a species-specific way is entrained to periods not too different from 24 hours by light and a few other stimuli. In interval timing, behavior is controlled by events of arbitrary periodicities considerably shorter than a day signaled in arbitrary ways. Whether short-interval timing also reflects one or more oscillators or is best understood in some other way is the subject of Section 9.3. This section summarizes the extensive data that provide the basic material for theories of timing. As we have seen already, concerns about time are intrinsic to the study of learning and memory. Recall, for example, the discussions of the role of time in conditioning (Chapter 4) and of whether animals remember events as occurring at particular times in the past (Chapter 7). But most explicit studies of interval timing have relied on operant conditioning procedures. A large body of such work is in effect psychophysics, asking how time is perceived. Based on that, often with similar experimental procedures, is research asking how perceived time controls behavior, for example when a signal to be timed is interrupted or when several events must be timed concurrently.

9.2.1 The psychophysics of time

The peak procedure, temporal generalization, and Weber's Law

Pavlov's demonstrations of inhibition of delay indicate that animals are sensitive to the time elapsed since a signal began. Operant studies using the *peak interval procedure* or simply *peak procedure* (S. Roberts 1981) tap interval timing in an analogous way. In this procedure, animals are exposed to many daily trials in which food can be earned a fixed time after the onset of a signal. For instance, in a procedure for pigeons, a pecking key lights and the first peck 20 seconds later is reinforced with food. The key then goes dark for an intertrial interval (ITI) of variable duration before lighting again to begin another trial with the same sequence of events. An omniscient pigeon need only peck once per trial, at the end of the programmed interval, but as pigeons are not omniscient and as they are typically fairly hungry in these experiments, they peck many times per trial and do so at a faster average rate as the time for food approaches.

To discover how precisely the animal knows the time of feeding, *empty trials* are added. These are occasional trials, maybe 20% of the total, in which no food occurs and the signal stays on perhaps twice as long as usual. Animals accustomed to this procedure respond most around the scheduled feeding time, as shown in Figure 9.6. Average response rates describe a nearly symmetrical normal distribution with its peak close to the interval being timed. When the interval to be timed is varied across animals or across blocks of sessions, a set of identically shaped curves results. The longer the interval being timed, the greater the spread of the distribution. If the x-axis of these plots is rescaled as proportion of the programmed interval and the y-axis as proportion of maximum response rate, the stretched or compressed response rate

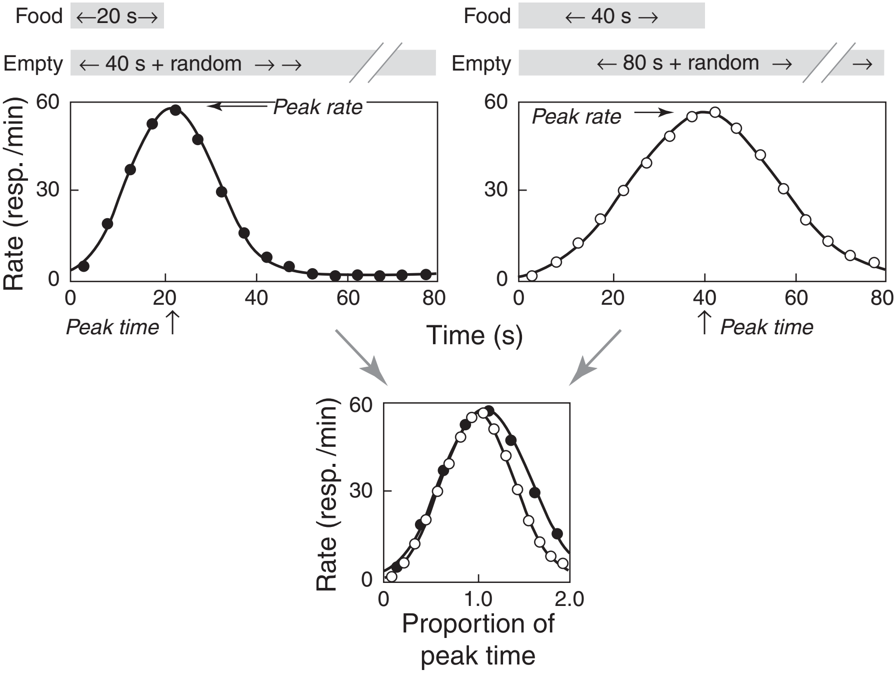


Figure 9.6. Examples of data from rats trained in the peak procedure with reinforcement 20 or 40 seconds after the beginning of the interval on food trials; no food was given on empty trials and the signal lasted longer than usual. The lower part of the figure shows how such data can be superimposed by rescaling the x-axis. The y-axis may also be scaled as proportion of peak rate. Redrawn from S. Roberts (1981) with permission.

graphs can be superimposed on one another (Figure 9.6). This means that for given species and testing conditions a predictable proportion of the maximum response rate is reached a certain proportion of the way though the interval regardless of how long the interval is. If we quite reasonably interpret an animal's rate of instrumental responding for food as an indication of how near in time it perceives the food to be, this result can be seen as an instance of Weber's Law (see Chapter 3). Longer times are perceived and/or remembered with greater variance than shorter times, and that variance is proportional to the duration being timed. This latter property is referred to in discussions of timing as *the scalar property* (Gibbon 1991).

One beauty of research on interval timing is that a variety of procedures produce mutually consistent results. For instance, in a test of temporal generalization responding is reinforced after a signal of one duration but not after other durations. In an early example with rats (Church and Gibbon 1982), the light in the operant chamber was turned off for a few seconds and then a lever slid into the chamber for five seconds. A rat was reinforced with food for pressing the lever if the period of darkness had been, say, four seconds, and not otherwise. This procedure yields a typical generalization gradient (Chapter 6) with its peak centered at the reinforced duration. Longer reinforced durations give broader gradients and, as in the peak procedure, these gradients are superimposed when the x and y axes are rescaled.

An animal tested with temporal generalization or the peak procedure can be seen as comparing a current interval with a memory of reinforced intervals in past trials.

Scalar timing indicates that this comparison is based on the ratio of current elapsed time or signal duration to the remembered interval. Equal ratios (i.e., equal proportions of the reinforced interval) lead to equal response rates or probabilities.

Bisecting time intervals

Further data consistent with ratio comparison come from tests of *temporal bisection.* Consider the following discrimination training procedure for rats. A tone comes on for either two or eight seconds. Then two levers slide into the operant chamber. Pressing the left lever is reinforced if the tone lasted two seconds, and pressing the right lever is reinforced if it lasted eight seconds. In effect, the rats are reporting their judgment of whether the tone is relatively short or long. When they are performing well, they can be tested with tones of intermediate durations. They divide their choices between the two levers in a predictable way, pressing the "long" lever on a higher proportion of trials the longer the tone is (Church and Deluty 1977). What is especially interesting is the duration at which they choose each lever 50% of the time, interpreted as the duration they perceive as halfway between long and short. Arithmetically, 7.5 is halfway between 3 and 12, but if animals compare time intervals by implicitly computing their ratios, the halfway or bisection point from the rats' point of view will be not 7.5 seconds but 6, as in fact it is (Figure 9.7). (The ratio of 12 to 6 is the same as the ratio of 6 to 3.) Another way to describe such findings is to say that the animals bisect the temporal interval at its geometric mean. (The geometric mean of two numbers is the square root of their product, for example, $6 = \sqrt{(3 \times 12)}$).

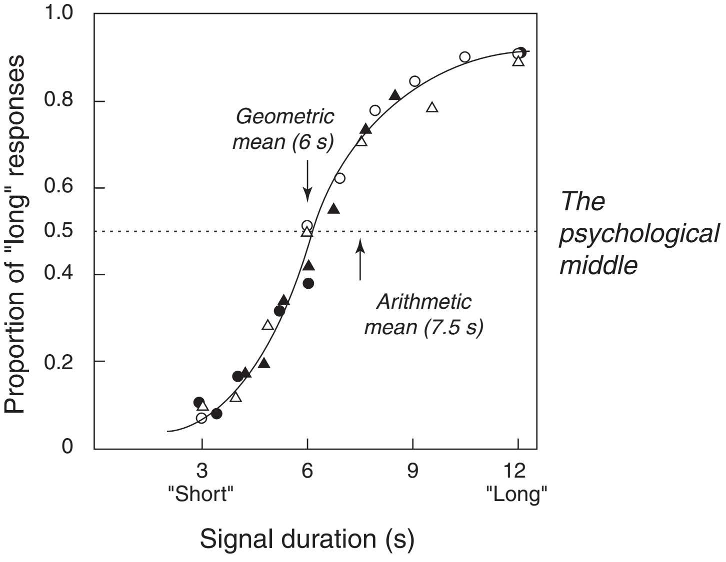


Figure 9.7. Results of a temporal bisection experiment in which rats were trained to press one lever after a 3-second signal ("short") and another after a 12-second signal ("long") and then were tested with intermediate durations. Different symbols represent different sets of test trials. Redrawn from Church and Deluty (1977) with permission.

Linear timing and time left

The foregoing discussion suggests that the length of an elapsing interval is perceived as a linear function of its actual length whereas times are compared in terms of their ratios. For instance, the first 10 seconds of a signal is subjectively the same duration as the last 10 seconds. An alternative possibility is that elapsed time is perceived logarithmically with real time, for example, 10 seconds late in an interval seems shorter than 10 seconds early in the interval (see Figure 9.8). With logarithmic timing, data consistent with the results presented so far would be obtained if perceived or remembered durations were compared arithmetically because equal ratios are equal intervals on a logarithmic scale. Some of the most direct evidence against logarithmic

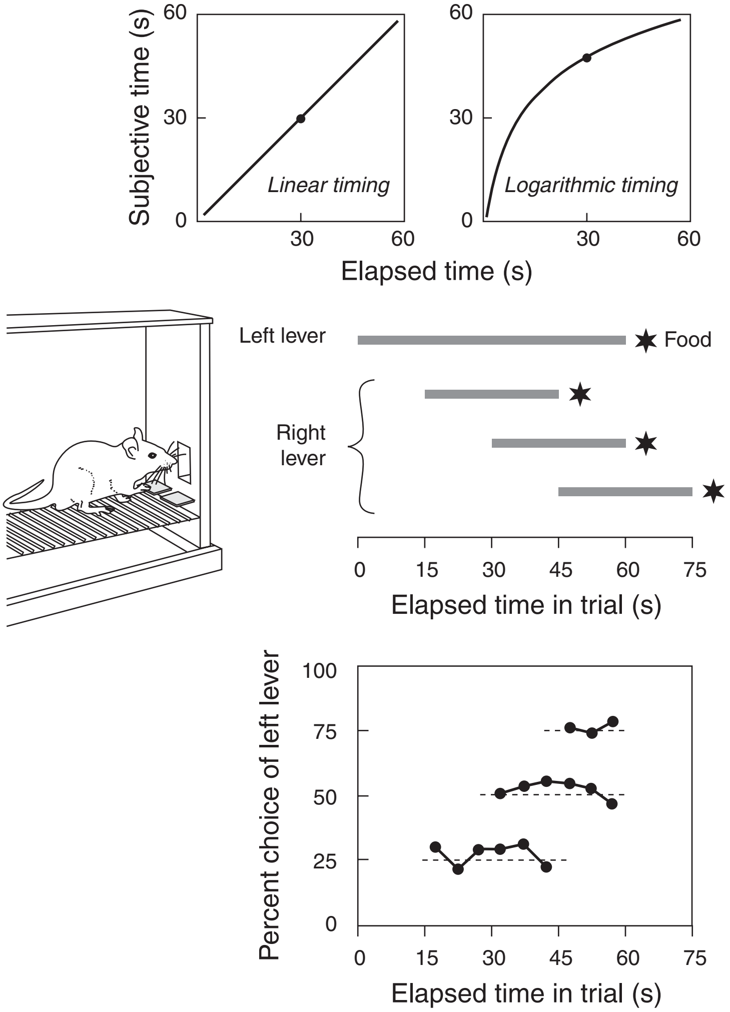


Figure 9.8. Top. How subjective time grows as a function of real time if timing is linear or logarithmic. Middle. Time left procedure for rats. Dark bars represent availability of the designated lever; stars are reinforcement. Bottom. Choice of the left, "time left," lever when the right lever enters 15, 30, or 45 seconds after the trial begins. Data redrawn from Gibbon and Church (1981) with permission.

timing comes from a clever test asking animals at any point at an elapsing interval whether they think the time left in that interval is more or less than a standard interval. The rationale for this *time left procedure* (Gibbon and Church 1981) is explained graphically in Figure 9.8.

In the time left procedure an animal is trained that one signal means food for a given response after one interval and a second signal means food for a second response after an interval half as long. Having learned to time these two signals, the animals are queried while they are working during the long signal, “Would you rather have food after the short signal than after the time left in this signal?” Suppose the long interval is 60 seconds and the short one 30 seconds. Clearly, the way to get food quickest is to choose the short signal when it is presented less than 30 seconds into the 60-second interval and choose what’s left of the long signal when it has been on for 30 seconds or more. Around the halfway point, animals should be indifferent between the two alternatives. But if time is measured logarithmically, the last 30 seconds of the elapsing 60-second interval will be subjectively less than the new 30-second alternative, and the animal’s choices will switch earlier than halfway through the 60 seconds.

Both rats and pigeons choose as predicted by linear timing (Gibbon and Church 1981; Figure 9.8). People do the same in an equivalent task involving choosing between hypothetical train journeys (Wearden 2002). However, just because the optimal choice can be computed by subtracting the elapsed time in the trial from the total time in the longer interval does not have to mean animals implicitly engage in an analogous process. Choice between two reinforcement schedules is traditionally thought to reflect what the animal has learned about the relative immediacy (inverse of delay) to reward on the alternatives at the time of choice. Variations on the time-left procedure developed within this framework are not so easily described in terms of subtracting representations of times to food (Cerutti and Staddon 2004; Lejeune and Wearden 2006). However, these findings do not necessarily undermine the linearity of timing, which is supported by many other data such as the appropriate location of peak responding in the peak procedure.

9.2.2 Using the clock

Timing with a gap

Sensitivity to the duration of a signal suggests that the onset of the signal starts a clock or timer of some sort (S. Roberts 1981). The results of typical timing experiments with many identical trials imply that this timer resets at the start of each new trial. If the timer were not reset or were only partially reset, successive presentations of the same signal could not be timed equally accurately. This description suggests that the mechanism for interval timing is like a stopwatch that starts running at the start of a new and interesting event and resets at the event’s end. So, like a stopwatch, can the timer be stopped and restarted without resetting? The answer to this question has been sought by seeing what animals do when a familiar signal of fixed duration is interrupted earlier than usual and restarted a few seconds later (Figure 9.9). For instance, suppose a rat is pressing a lever for food during a 30-second tone and the tone is interrupted briefly 10 seconds after its onset. When the tone comes on again, will the rat respond at the rate characteristic of 10 seconds into the interval and peak 20 seconds later, or will it start again from zero and peak 30 seconds after the gap in the signal? The former would indicate that the rat’s interval timer had been stopped

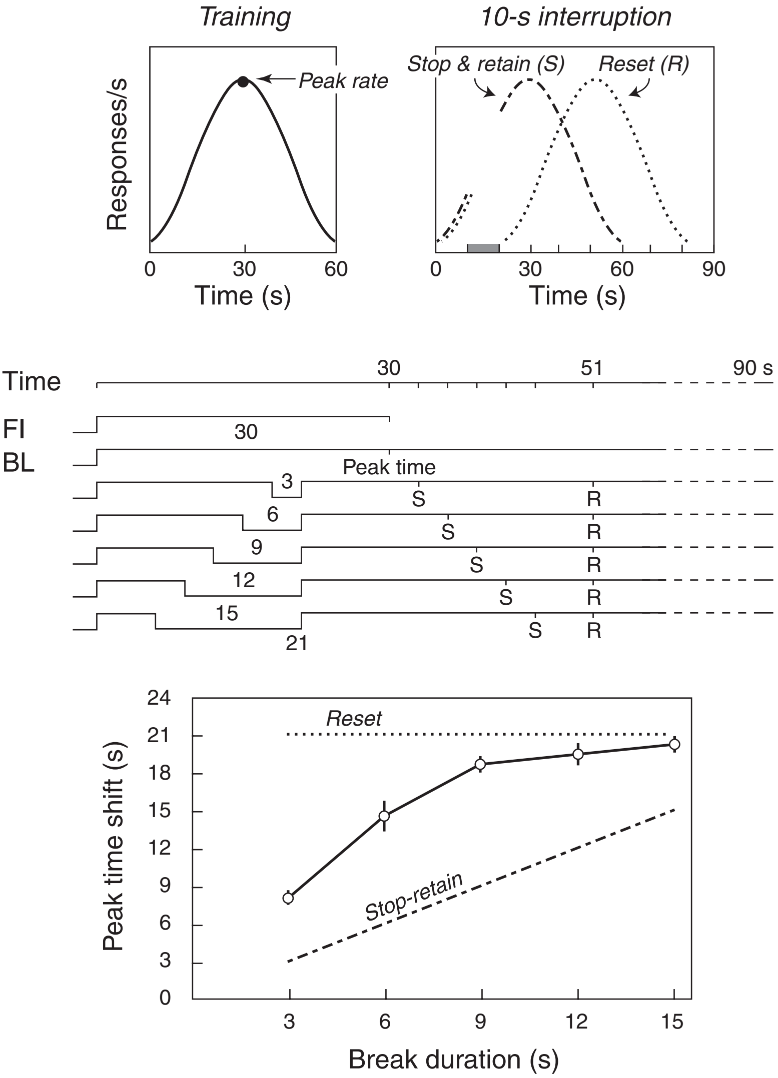


Figure 9.9. Top. Two hypothetical results of training on a 30-second peak procedure and then interrupting the 30-second signal for 10 seconds. The clock timing the interval may either stop during the interruption and retain the duration before the interruption (S) or it may reset (R). Middle. Peak times, in seconds from the start of the interval, predicted by the two models for an experiment with interruptions of different lengths programmed to end at the same point in the interval. FI fixed interval after which food was delivered; BL blank trial, no food. Bottom. Predictions and results for an experiment with pigeons following the design above. Redrawn from Cabeza de Vaca, Brown, and Hemmes (1994) with permission.

and restarted, the latter that it had been reset at the gap. And of course the rat might show peak responding at the usual time after the original onset of the signal, as if its timer kept running through the gap.

At one time it appeared that the results of such experiments depended on the species being tested. Rats resumed timing after a gap (S. Roberts 1981), whereas pigeons reset (W. Roberts, Cheng, and Cohen 1989). However, as often happens in such cases, it turns out that procedural variations can produce the same range of outcomes with one species (Cabeza de Vaca, Brown, and Hemmes 1994; Buhusi, Sasaki, and Meck 2002; Buhusi, Perera, and Meck 2005). Why resetting occurs in some conditions and not others has had several explanations. For example, to time an interrupted signal accurately, it is necessary to retain an accurate memory of the time that elapsed before the gap and add the time after the gap to it. Forgetting the time before the gap leads to apparent resetting. This insight predicts that the extent of resetting should depend in a continuous way on the size of the gap. The longer the gap, the more the first part of the signal is forgotten and the later in the resumed signal is the peak time of responding. This prediction was supported in an elegant series of experiments with pigeons (Cabeza de Vaca., Brown, and Hemmes 1994). But the salience of the gap also turns out to be important. For example, smaller changes in the intensity of a light or tone lead to smaller delays in peak responding, as if timing continues through the gap (e.g., Buhusi, Sasaki, and Meck 2002). Such delays also result if a brief distractor is presented while the signal being timed continues uninterrupted, for example, a noise sounds while a light is being timed (Buhusi and Meck 2006). In the initial experiments in this area, the gap was indistinguishable from an intertrial interval, and because animals in these studies have in effect been trained extensively to erase their memories and start timing afresh at the end of each ITI, resetting after such a gap is to be expected (Zentall 2006). However, the insight that the gap is ambiguous in this way does not appear to account for all the relevant findings. Rather, if timing an ongoing signal is viewed as a working memory task, it can be seen that distracting the animal's attention leads to gradual decay of memory for the time already elapsed, more so the greater the salience of the distractor (Buhusi and Meck 2006). This process-based approach seems more likely to explain what is going on here than is appeal to the metaphor of a stopwatch (see also Staddon and Cerutti 2003).

Timing multiple events

The fact that animals of a given species can time both lights and tones means that different modalities have access to the interval clock. Moreover, timing transfers from one signal to another, novel, signal in a different modality (W. Roberts., Cheng, and Cohen 1989), suggesting that a single timer tracks events within a trial. But animals are also capable of timing two or more concurrent events, as if using multiple timers simultaneously. For instance, pigeons can learn that food occurs at either of two different points within a signal. If food does not appear at the shorter of the two intervals, responding falls, as in the peak procedure, and then rises again as the end of the longer possible interval approaches (Leak and Gibbon 1995). And in laboratory studies of foraging (see Chapter 11), pigeons time the length of foraging bouts while keeping track of the durations of several events within them (e.g., Plowright 1996).

One impressive example of timing multiple events comes from a field study in which rufous hummingbirds (*Selasphorous rufus*) found artificial nectar in an array of eight differently colored feeders (Henderson. et al. 2006). Like real flowers, the experimental "flowers" quickly depleted of nectar but replenished a predictable time later. In this case, four randomly selected flowers in the array replenished after ten minutes and the other four after twenty. The birds learned to time their visits appropriately, as measured by the times between a reinforced visit to a flower and the next visit to that flower. This means not only that they were able to learn the refill rates of eight separate flowers but that throughout the day they were updating their memories of how long ago they had visited each one, in a process that shares elements of the episodic-like memory discussed in Chapter 7. However, because real flowers may take much longer than 20 minutes to replenish (Castellanos, Wilson, and Thomson 2002; Stout and Goulson 2002), to be useful in nature the ability demonstrated by Henderson et al.'s birds might have to be scaled up in numbers and durations of events.

Integrating time with other cues

The hummingbirds' behavior provides but one example of how information about comparatively short intervals is normally combined with other cues, in this case location. A less dynamic form of time and place memory has been documented in numerous laboratory studies analogous to daily time and place learning but using shorter sessions (Thorpe and Wilkie 2006). For example, pressing one lever might be reinforced for the first 15 minutes of a session and pressing another lever reinforced for the next 15 minutes. The integration of interval timing with other information has been explored in a different way by by teaching pigeons and people to respond when a moving shape on a video monitor reached a certain position on the screen (Cheng, Spetch, and Miceli 1996). During training, the shape always moved at the same speed, so subjects could respond to its position, the time since it started to move, or both. When the stimulus moved faster or slower than usual, both the pigeons and the people appeared to respond to both temporal and spatial information and average them when they conflicted. In circadian time-place learning, by contrast, animals learn both the time and the place of important events, but it is not clear what averaging this information could mean.

Chapter 4 provides extensive evidence that animals are always processing information about the durations of interesting events and the intervals between them. Recall, for example, that the distribution of trials in time is critical for conditioning and that temporal information such as when the US occurs during the CS is part of what is learned (see also Arcediano and Miller 2002). Moreover, this information may be acquired in a single trial of fear conditioning (Davis, Schlesinger, and Sorenson 1989) and almost as quickly in other conditioning settings (Balsam, Drew, and Yang 2002). Temporal information appears to be especially powerful when used as an explicit associative cue, for example not being readily blocked (Williams and LoLordo 1995). These facts are relevant to evaluating theories of interval timing in Section 9.3.

9.2.3 Summary

The two most important properties of interval timing are (1) subjective time grows linearly with real time and (2) timing obeys Weber's Law (or has the scalar property, Lejeune and Wearden 2006). Perception of time therefore shares both linearity and conformity to Weber's Law with perception of other features of the world such as space. Interval timing also shares with spatial cognition its sensitivity to multiple sources of information (Cheng 1992).

The most analytical experiments on interval timing have been done with rats and pigeons. Many of the procedures used have been adapted for humans, with similar results (Wearden 2002; Meck 2003). Comparable data from a rodent, a bird, and a primate along with data from other species (Lejeune and Wearden 1991) are suggestive of pretty wide phylogenetic generality among vertebrates. Bumblebees also show evidence of timing short intervals (Boisvert, Veal, and Sherry 2007). These data consist mainly of patterns of responding on *fixed interval* (*FI*) *schedules*, which are essentially the same as the peak procedure but without the empty trials. The increases in response rate as reward approaches may not be equally sharp in all species. Turtles, for instance, have a much shallower slope than monkeys or rats, suggesting that they do not perceive interval duration as accurately. However, the apparent precision of interval timing can also vary within a species with motivation (Plowright. et al. 2000) and with the response used to index timing. More effortful, costly, responses may lead to apparent increased accuracy. For instance, pigeons appear to time more accurately when they hop on a perch for food than when they peck (Jasselette, Lejeune, and Wearden 1990). Attempting to capture species differences in a model including both response mechanisms and sensitivity to time leads to the conclusion that species differ in both (Lejeune and Wearden 1991). Ecological hypotheses about species differences in accuracy of interval timing have apparently not been tested.

9.3 Interval timing: Theories

For over 20 years, a particular cognitive model, the information processing or pacemaker-accumulator model (Gibbon and Church 1984), has dominated discussion of the processes underlying performance in tests of interval timing. Indeed, the assumptions of this model are reflected in some of the tests already described. More recently, fundamentally different alternatives have been proposed that account for interval timing without a pacemaker and accumulator and in some cases without explicit sensitivity to time as such. Two are described here. Each has stimulated new experiments with results that the information processing model cannot readily account for.

9.3.1 The information processing model

This model is also known as *Scalar Expectancy Theory* (SET; Gibbon 1991) or the pacemaker-accumulator model. The model's general structure (Figure 9.10) has much in common with the structure of the memory model of habituation (Chapter 5) and models in other realms of cognition (Church and Broadbent 1990) in which behavior is based on comparing a current event to a representation of past events. It has three major components, or modules: a clock that measures current time linearly, a memory for storing durations of past events, and a comparator for comparing current time to remembered time. The clock rests on a hypothetical pacemaker that is assumed to generate pulses at a fairly high rate. The onset of a signal to be timed switches these pulses into an accumulator, a working memory that tracks the duration of the signal. The comparator computes the ratio of the value in the accumulator to the value of reinforced time in reference memory and outputs a decision about whether the current time is acceptably close to the remembered time. Behavior is generated in an all-or-nothing way depending on whether or not the ratio exceeds this decision threshold. This last conclusion is based on the fact that rats and pigeons do not increase responding gradually as the time for reinforcement approaches on single trials of the peak procedure. Rather, responding has a *break-run-break* pattern, that is, at a certain point in the trial the animal switches suddenly from a very low rate of responding to a high steady rate. In empty trials, it maintains this rate until after the time of reinforcement, and then there is another break in responding. The run of responding is seen as beginning at the point where the ratio of current time to remembered time of reinforcement exceeds the threshold, and the break in responding at the end of the run reveals when the ratio falls below the threshold again (Cheng and Westwood 1993; Church, Meck, and Gibbon 1994).

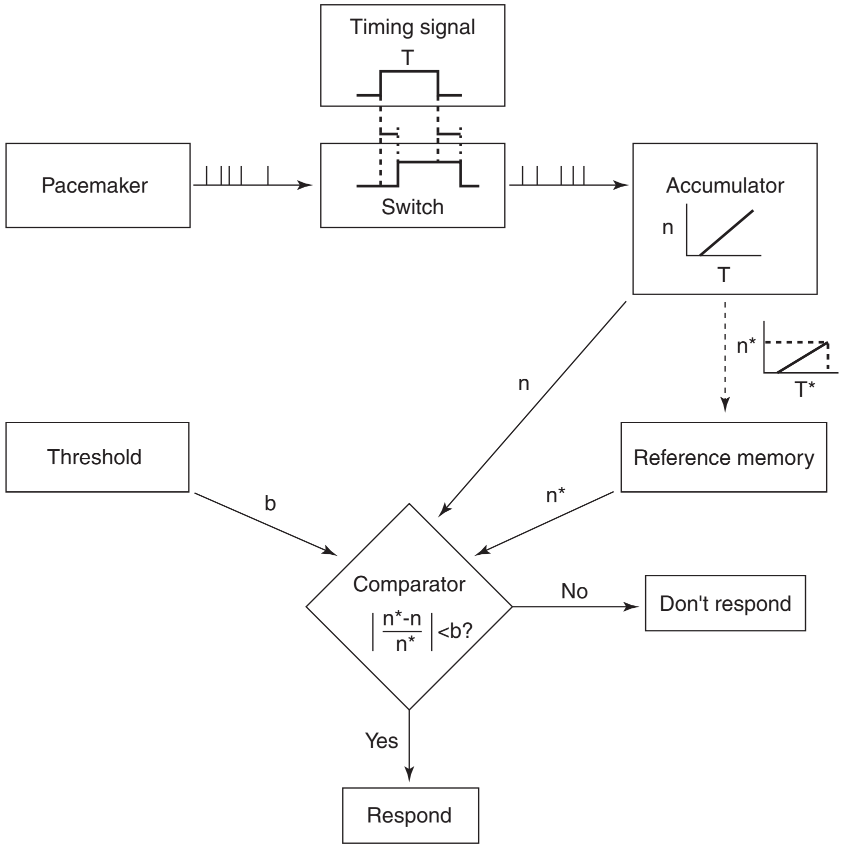


Figure 9.10. The information processing model of timing. n*: number of pulses on reinforced trials, the value stored in reference memory. Redrawn from Church, Meck, and Gibbon (1994) with permission.

In terms of the model, why is timing scalar, that is, why does the variance in temporal generalization, the peak procedure, and the like increase with the length of the interval being timed? The source of this variance cannot be the operation of the switch that causes an event to be timed because the switch is assumed to close just once, at the start of the timed event, and open again at the event's end. Any variability in the latency of the switch's operation would be constant regardless of the length of the interval to be timed. Variability in the speed of the pacemaker, on the other hand, could produce scalar variance because it would influence the total number of pulses in working memory more in long intervals than in short ones. There are other possibilities as well, not all of which are easy to disentangle from one another experimentally.

The pattern of responding on single trials reveals the moment-by-moment dynamics of the decision process (Cheng and Westwood 1993; Church, Meck, and Gibbon 1994). For instance, different, possibly variable, thresholds may be used to decide when to start responding and when to stop. These analyses also indicate that a single sample is taken from the memories of times to reinforcement in reference memory and compared continuously to the time in the accumulator. The notion that a distribution of experienced times to reinforcement is stored in reference memory and sampled on each trial can be distinguished from the possibility that reference memory is an average time to reward, a single quantity updated with each new experience. Storing a continually updated average seems cognitively less demanding than storing a distribution. Nevertheless, as we will see in Chapter 11, a model based on memory for the distribution of intervals accounts very well for a number of kinds of foraging decisions.

9.3.2 The oscillator model

Just as in analogous models of other memory processes, the structures represented in Figure 9.10 are purely hypothetical, analogues to physical structures that could produce outputs matching real data in timing experiments. Such models have served cognitive psychology well, but they are not necessarily biologically realistic. One way to make a biologically more realistic model of timing is to replace the pacemaker plus accumulator with a system of oscillators and status indicators, as originally suggested by Gallistel (1990). The physiology and behavior of most organisms provide evidence of numerous biological oscillators driving repetitive motor patterns like flapping, walking, or licking, and rhythmic functions like heartbeat and breathing (Buhusi and Meck 2005). It is plausible that they include the sorts of oscillators necessary for interval timing. Rather than counting pulses, the oscillator model records the state of each of a set of oscillators of different periodicities, as shown in Figure 9.11. One or more of these may have a period longer than a day, perhaps months, years, or the animal's lifetime. Thus a great appeal of the oscillator model of interval timing is that it unifies timing at all scales in terms of a single set of oscillators.

Figure 9.11 shows why more than the single circadian oscillator is needed to do this job. Because intervals of the order of seconds or a few minutes are just a tiny fraction of a day, timing them accurately with the circadian oscillator would require discriminating tiny changes in the phase of that oscillator. A good solution is to this problem is to record the state of a number of oscillators, each of which oscillates about twice as fast as the next slower one. In this model, interval timing is not counting pulses but recording the times of a signal's onset and offset in terms of oscillator status indicators and computing duration from this information. Accordingly, the oscillator model is compatible with evidence that interval timing involves detecting coincident activity in multiple areas of the brain (Buhusi and Meck 2005).

A key prediction of an oscillator model is that intervals close to the period of one of the oscillators should be more discriminable than slightly longer or shorter intervals, that is, "oscillator signatures" should be detectable as systematic deviations from

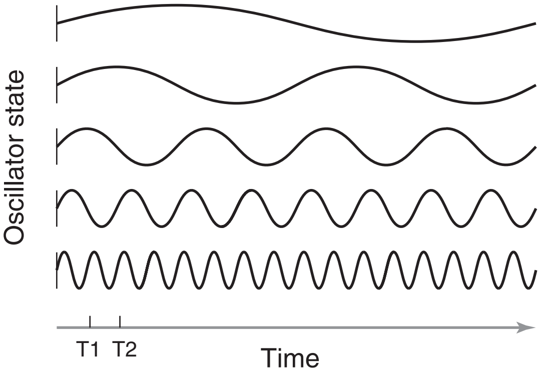


Figure 9.11. Timing with oscillators. Each oscillator has a period half that of the next slower. Unambiguously distinguishing T1 from T2 requires reading the status of all the oscillators (i.e. the height of each sinusoidal line) at both times.

scalar timing. A nice proof of principle for this suggestion comes from training rats with interfood intervals with lengths around the period of a known oscillator, the circadian rhythm (Crystal 2001). Each rat, kept in constant darkness, could earn food within a three-hour period with a fixed intermeal interval between 14 and 34 hours long. (As mentioned in Section 9.1, circadian rhythms do not entrain to the extremes of these intervals, but they can acquire control of instrumental behavior.) For all the intervals, insertions of the rat's head into the food magazine increased during the few hours before food was due, but the data did not superimpose when they were rescaled as proportions of the interfood interval. Instead, as predicted by oscillator theory, the sharpest increases (i.e., best discrimination) were found for the intervals closest to 24 hours.

The applicability of this approach to short interval timing is illustrated by a study in which rats learned a *ramped interval* schedule (Crystal, Church, and Broadbent 1997; Crystal 2006a). This is essentially a fixed interval procedure except that each interfood interval was two seconds longer than the preceding one within a given range between 20 and 160 seconds. When the longest interval in the range was reached, the intervals ramped down again two seconds at a time. Animals do learn such a contingency, as shown by systematically changing pauses between feeding and beginning to respond again. The ramped schedule used here allowed timing of many closely spaced intervals to be assessed. As predicted by oscillator theory, the data showed systematic deviations from a linear relationship between start times and the duration of the interval to be timed. Greatest accuracy was around 10 to 12 seconds and 100 to 120 seconds. The generality of these periodicities to other tests and/or other species remains to be determined (but see Crystal 2006a). To a first approximation, scalar timing remains a good account of many interval timing data (Lejeune and Wearden 2006), but these violations suggest that the underlying measurement of time might not involve a pacemaker and accumulator.

Notwithstanding the appeal of an approach that integrates interval and circadian timing by calling on a common process of biological oscillation, its support by actual biological data is mixed. For example, rather than reflecting a unitary mechanism in the brain, circadian and interval timing are dissociable by brain lesions. In mammals, removing the suprachiasmatic nucleus abolishes daily rhythmicity but leaves interval timing intact, whereas interval timing depends on an intact striatum (see Buhusi and Meck 2005). Furthermore, learning about short intervals is not the same as entrainment of circadian rhythms. For instance, although there is some evidence that temporal patterns of behavior persist when regular reinforcement is discontinued (Crystal 2006b), there is not yet evidence for free-running short-interval timers. At the same time, neurobiological support for the information processing model comes from the fact that some of its components such as clock speed and memory can be dissociated pharmacologically. However, studies of brain activity during timing tasks provide increasing evidence that short-interval timing involves detection of coincident activity in multiple brain regions, more consistent with the oscillator model (Buhusi and Meck 2005; Bhattacharjee 2006).

9.3.3 Timing without a clock: Behavioral theories of timing

Describing the control of behavior by temporal patterns of reinforcement has been a staple of the study of operant conditioning since long before cognitive models appeared (Staddon and Cerutti 2003). The Skinnerian tradition of eschewing explanations of behavior in terms of unobservable internal processes is reflected in the

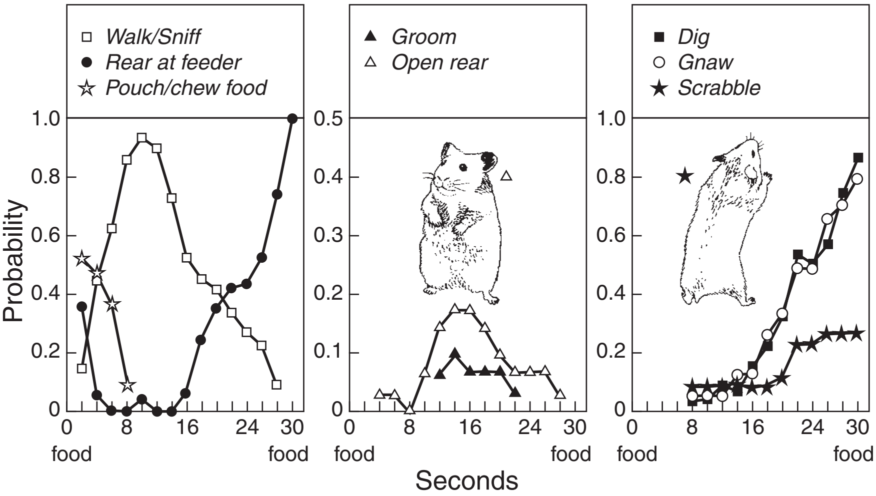


Figure 9.12. Typical behavior of golden hamsters given food every 30 seconds in an open field. Some activities appear reliably just before or after feeding whereas others (the adjunctive behaviors) are performed most in the middle of the interfood interval. Data from one animal, redrawn from Anderson and Shettleworth (1977) with permission; hamsters from Shettleworth (1975) with permission.

behavioral theory of timing (or BeT; Killeen and Fetterman 1988). This approach does not assume that animals count pulses or record states of oscillators, much less that they perform implicit computations on such hypothetical entities. It is an attempt to account for behavior that has seemed to demand a cognitive explanation in purely behaviorist terms, indeed, to account for timing without a clock.

Inspiration for the behavioral theory of timing comes from observations of *adjunctive behaviors* that develop when animals are exposed to food deliveries spaced regularly in time regardless of behavior (*fixed-time schedules*). Immediately after each food delivery, animals tend to engage in behaviors unrelated to food such as grooming and walking about. As the interfood interval progresses, food-related behaviors such as gnawing or pecking in the vicinity of the feeder come to predominate (Figure 9.12). In the language of Chapter 4, activities in the feeding system are performed late in interfood intervals and behaviors from other systems, such as grooming or exploration are performed at other times. In the language of the behavioral theory of timing, the succession of adjunctive behaviors reveals a series of underlying states. Unlike in the example of adjunctive behavior, these states are not specified in terms of feeding or other motivational systems, nor in terms of anticipation of the time of food delivery. Accurate choice or appropriate response rates in operant experiments like the peak procedure or temporal discrimination arises because responding is associated with a particular state in the sequence (Figure 9.13).

When food is more frequent, animals generally appear more excited, switching from one activity to another more often, suggesting that the states succeed each other more rapidly the higher the rate of food presentation. This means that short intervals are timed more accurately than long ones, that is, timing is scalar, just as it should be. This should be true only if the short intervals are generated in a way that increases the average rate of feeding in the experimental context, as when the intertrial interval in

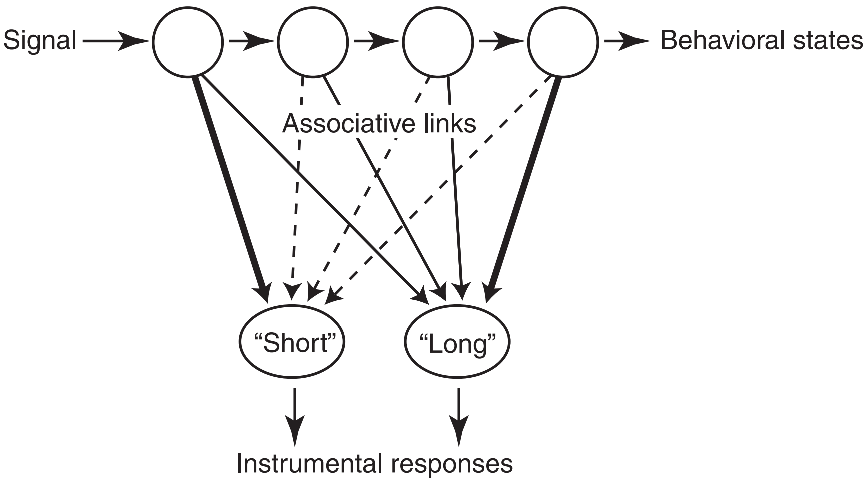


Figure 9.13. The learning to time (LeT) model. Onset of a signal instigates the first in a sequence of behavioral states (top row of circles), each of which may become associated with one or more instrumental responses. Here the responses are identified with a short and a long elapsed time, as in the temporal bisection procedures discussed in the text. After Machado and Keen (1999) with permission.

the peak procedure remains constant while the interval to be timed is shortened. BeT does not predict that the scalar property will be maintained when multiple intervals are being timed concurrently, but in fact it is (Leak and Gibbon 1995). Note too, that no explanation is given for why and how states succeed one another, but in effect their succession plays the role of a pacemaker (Hopson 2003). On a cognitivist view, of course the behavioral "states" are merely the readouts of an internal clock.

The behavioral theory of timing along with its mathematical development as the Learning to Time theory (LeT; Machado 1997) accounts for all the basic phenomena described in Section 9.2. Because it was designed to account for average data, it does not (as yet) account for the timing of breaks and runs in responding on individual trials of the peak procedure, whereas these have a natural interpretation in SET (Church., Meck, and Gibbon 1994). LeT has stimulated a series of studies with the *double bisection* procedure, with dramatically different results from those anticipated by SET. Recall that in temporal bisection an animal is trained to make one response after a comparatively short signal, say a 1-second light, and another response when the same signal has lasted some longer time, say 4 seconds. In tests with intermediate durations, the proportions of trials with each response are seen as revealing the animals' ratings of how similar the duration is to each of the training durations. In terms of SET, onset of the signal causes pulses to flow to the accumulator. At the end of the signal, the total in the accumulator is compared (as a ratio) to the reference memories of the totals associated with each of the choices.

Now consider training two temporal discriminations concurrently. For example, at the end of a 1-second or 4-second white light, pigeons are offered a choice between red and green, with red correct after 4 seconds and green otherwise. On other trials within the same session, the same white signal comes on for 4 seconds or 16 seconds, and the pigeons choose between blue and yellow, with blue correct after the 4 second light. According to SET, if the pigeons are now presented with the 4-second light, or indeed a light of any duration at all, and given the novel choice between red and blue, they should be indifferent because both are associated with the same state of the accumulator. According to LeT, however, choice will depend on the duration of the test signal, as in fact it does (Machado and Pata 2005).

To understand the predictions of LeT, call the two discriminations 1 and 2 and the choices associated with the comparatively short (S) and long (L) intervals respectively S1 and L1, S2 and L2. In our example, L1 and S2 are both associated with the same 4-second signal. According to LeT, onset of the signal initiates a series of behavioral states such as first moving to the left side of the chamber, then turning around, then pecking at the front panel. Such idiosyncratic stereotyped behavioral sequences are often (but not always) observed in pigeons (e.g., Machado and Keen 2003). To understand the double bisection results, we need three states, the initial state, in effect for the first second or two after the light comes on, the intermediate state, and the final state, beginning some time after 4 seconds or so. In discrimination 1, in the presence of the initial state choices of S1 are reinforced and choices of L1 (the 4-second option) are explicitly extinguished. L2 and S2 are neither reinforced nor extinguished during the initial state because the earliest they occur is after 4 seconds of the signal, in discrimination 2. Therefore, when L1 and S2 (the two 4-second options) are presented during the initial state, S2 will be chosen because it has not been extinguished under these conditions whereas L1 has. Extending this argument not only correctly predicts that L1 will be chosen over S2 in the presence of the final state, that is, when the two supposedly equivalent 4-second options are presented after a signal longer than 4 seconds, but also makes interesting (and correct) predictions for choice between other novel pairs (Machado and Pata 2005). However, thinking in terms of times on a clock (as opposed to behavioral states) when the various options are reinforced or not may provide just as good an account. In our last example, after times much greater than 4 seconds choice of S2 should be inhibited because it is never reinforced at such times; hence the alternative, L1, is chosen.

9.3.4 Cognitive and behavioral theories of timing: Conclusions

The oscillator and the LeT/BeT models are not the only alternatives to SET than have been proposed. Other accounts of behavior in timing experiments include Kirkpatrick's (2002) packet theory, models based on neural networks (Hopson 2003), and Staddon's (2005) memory model. Like some neural nets, Staddon's model has no representation of time as such. Important events such as feedings create a memory trace that decays in a predictable way, as in habituation, and the strength of this trace acts as a clock. In the simple example of a fixed-interval 10-second schedule, the next feeding occurs when the trace of the most recent feeding has decayed to a level typical of 10 seconds post-feeding. Multiple traces are needed to generate behavior in more complex situations, not always successfully (Church 1999, 2001; Hopson 2003).

The contrast between explanations at a purely behavioral level and those that call on cognitive mechanisms is exceptionally clear in the area of interval timing. There is currently no consensus about which provides the most comprehensive account of interval timing, but rather respectful acknowledgement that fundamentally different theoretical approaches can satisfactorily account for the major patterns of data, at least within explicit tests of timing (Church 2001; Staddon and Cerutti 2003; Church 2006; Lejeune and Wearden 2006). And the various explanations of timing are not entirely mutually exclusive. For example, it seems possible that when animals are trained with signals predicting food at fixed times, they initially time the signals but once rigid stereotypes develop those behaviors become directly associated with choice responses as depicted in LeT.

Each of the three models discussed in Sections 9.3.1–.9.3.3 can account uniquely well for some subset of data (e.g., nonlinearities in short-interval discriminations for oscillator theory; performance on double bisection for LeT). Evidence from neuroscience may contribute to deciding among candidate mechanisms, for example by increasing the plausibility of a multiple oscillator system. Another consideration that does not seem to have received much attention is functional plausibility. On one view (Gallistel 1990, 2003), sensitivity to time is a core aspect of animal information processing. Spontaneously recording circadian and interval times is obligatory and absolutely fundamental to learning and memory. For example, sensitivity to durations in the seconds to minutes range underlies conditioning (Chapter 4; Gallistel and Gibbon 2000; Arcediano and Miller 2002). From this viewpoint, the behavioral theory of timing (LeT included) is decidedly implausible because it is designed to explain behavior that develops after extensive exposure to rigid and arbitrary sequences of events without assuming any underlying sensitivity to time as such. The stereotyped behavior that may develop under these conditions (e.g., Machado and Keen 2003) hardly seems to provide a primary mechanism for spontaneously recording in some fashion the durations and times of occurrence of interesting events in the messy quotidian flow of experience, even though there is evidence that animals do just that (M. Davis, Schlesinger, and Sorenson 1989; Balsam, Drew, and Yang 2002). The pacemaker-accumulator or oscillator models, and perhaps Staddon's memory-based model, are better able to do this job.

9.4 Summary: Two timing systems?

Notwithstanding attempts to link them in a single system of biological oscillators (Crystal 2006a), circadian and interval timing can be seen as two functionally and causally distinct information-processing systems or modules. (Learning serial order is a third mechanism for organizing behavior in time, as in adopting a daily foraging routine, but, unlike circadian and interval timing, ordinal timing (Carr and Wilkie 1997) does not involve responding to time per se.) The circadian timing system consists of an endogenous oscillator with a period of about a day that is normally entrained by light or one of a few other biologically important events. The circadian oscillator runs freely in the absence of effective entraining agents, and although cells throughout the body have circadian rhythms, in mammals the master oscillator is located in the suprachiasmatic nucleus. A primary function of the circadian system is to adjust the animal's behavior to local day and night. Among other things, it allows animals to learn when and where food is regularly available.

The function of interval timing, in contrast, is to adjust behavior to important events with durations much shorter than a day. Unlike day and night, the durations and times of occurrence of these events are not predictable in advance of individual experience, and they can take on any value. Intervals too short to reasonably discriminate in terms of phase of the 24-hour cycle can be timed accurately. Furthermore, developing a regular sequence of behavior after experiencing a sequence of events that is predictable on the scale of seconds to minutes does not occur through entrainment. In entrainment, the underlying rhythm runs freely and is brought into register with the environmental rhythm as described by a phase response curve. It has a restricted range of entrainable phases. This description does not readily apply to learning of short intervals, although it has hardly had a fair test (see Crystal 2006a).

There is a single generally agreed on model of circadian timing, but several such models of interval timing. One of these, the oscillator model, links circadian and interval timing as different expressions of a single set of oscillators with phases ranging from seconds to multiples of days. However, it does not appear to account for the unique characteristics of the circadian oscillator just reviewed. Although the alternative theories of timing are likely to go on generating challenging data, scalar expectancy theory still appears to provide the most powerful account of all aspects of interval timing. SET reappears in Chapter 11, where it provides a useful account of how animals assess and compare rates while foraging.

Further readings

An authoritative as well as amusing brief introduction to circadian timing is the article by Aschoff (1989), one of the founders of the field. The text by Moore-Ede, Sulzman, and Fuller (1982) is still an excellent introduction to the classic work on biological rhythms. Understanding the genetic control of circadian rhythmicity is one of the greatest success stories in the molecular analysis of behavior; it is described in more recent texts such as *Chronobiology* (Dunlap, Loros, and Decoursey 2003). Chapters 7–9 of Gallistel (1990) discuss both circadian and interval timing from the author's "computational representational" point of view. Thorpe and Wilkie (2006) review time and place learning.

A good introduction to interval timing is the chapter by Russell Church (2002), one of the founders of the field and originators of SET. Church (e.g., 2001, 2006) has also written some thoughtful assessments of the alternative approaches. Staddon and Cerutti's (2003) review of operant conditioning includes a major section on behavioral approaches to interval timing, and Crystal (2006a) reviews studies testing the oscillator model. Arcediano and Miller (2002) summarize the challenges for timing theories from evidence that times are learned during conditioning. Neural bases of timing as well as behavioral studies are discussed in the book edited by Meck (2003) and summarized by Buhusi and Meck (2005; see also Bhattacharjee 2006).

10
Numerical Competence

Readers who know the story of Clever Hans will know that whether animals can count is one of the oldest questions in the experimental study of animal cognition. Clever Hans was a German horse in the early 1900s who answered questions about numbers by tapping with his hoof (Pfungst 1965; Candland 1993). Although a committee of thirteen eminent men was satisfied that Hans really could count, investigations by the young experimental psychologist Oskar Pfungst revealed otherwise. Hans *was* clever, but not in the way he originally appeared to be. He proved to be responding to slight unconscious, movements of questioners who knew the correct answers. Clever Hans's legacy is a name for any effect that reflects responding to cues unintentionally provided by experimenters and a widespread skepticism about any studies in which animal and experimenter interact directly.

Notwithstanding the Clever Hans affair, research on animal counting continued throughout the twentieth century (Rilling 1993), increasing in the 1970s along with research on other aspects of comparative cognition (reviews in Davis and Memmott 1982; Boysen and Capaldi 1993; Shettleworth 1998; Boysen and Hallberg 2000). Toward the end of the century, however, the theoretical focus of research on animals' numerical abilities shifted away from the simplistic "can animals count?" toward a more nuanced view of numerical competence as comprised of several systems shared among species to different degrees, with a language-based system unique to humans. The contemporary study of numerical cognition is a rich area of interaction among comparative and developmental psychologists as well as cognitive neuroscientists, sometimes embodied in the same individual researcher or research team. Much of this progress rests on the fact that babies and monkeys, and to some extent other animals, can be given virtually identical nonverbal tests of sensitivity to number.

To appreciate the way in which the comparative study of numerical abilities has evolved, it is worth briefly reviewing older studies of animal counting. In counting, each member of a set is tagged ("one," "two," "three," . . .). These numerical tags are *numerons* (Gallistel 1990). They are applied in a fixed order, but the order in which the items in the set are counted doesn't matter as long as each item gets one and only one tag. The final tag is the *cardinal number* of the set, the number of items in it. True counting implies transfer of the same numeron to sets of all sorts of things in all sorts of arrangements, that is, counting transcends features normally confounded with number such as total extent of items in the set. Numerons need not be words in any human language. Animals' number tags can be "unnamed

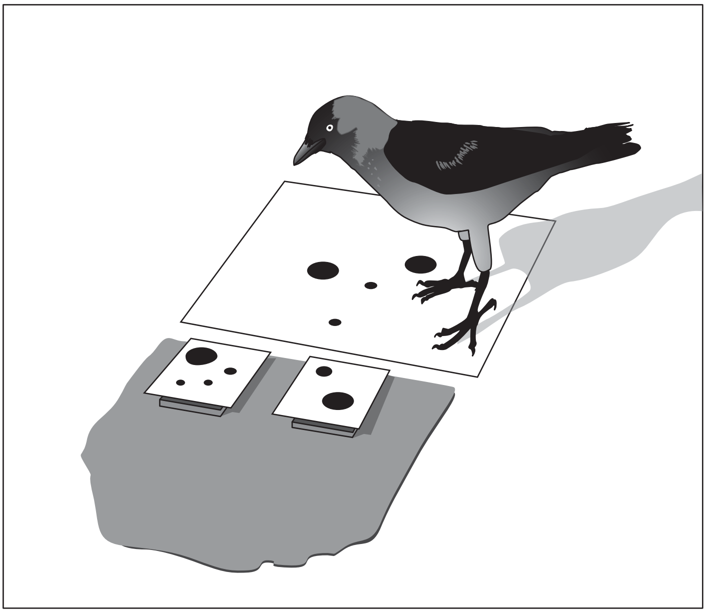


Figure 10.1. A jackdaw being tested for the ability to match numbers of items. The small squares are lids on food pots; here if the bird flips over the one with the same number of dots as on the large card it will find food underneath. After a photograph in Koehler (1941).

numbers" (Koehler 1951). The ability of birds to use such tags was studied extensively by Koehler (e.g., 1951; see also Davis and Memmott 1982; Emmerton 2001). For example, he trained parrots, jackdaws, and other birds to match drawings according to the number of items they contained, disregarding size and arrangement (Figure 10.1). He also trained birds to eat a fixed number of items from a pile by shooing them away when they reached the criterion, a demonstration later performed with rats by H. Davis and Bradford (1986). H. Davis (1984) also trained a raccoon to select the one box out of five that had three items of food or three other objects in it, and Capaldi and his colleagues (Capaldi and Miller 1988; Capaldi 1993) showed that rats readily learn to expect food at the end of a runway on two or three trials in a row and no food on a final trial.

In all these examples, "counting" consisted of discriminating a set of one small size from sets of other small sizes, and indeed Koehler reported that his birds failed such tasks when the number involved was greater than six or seven. Some of Koehler's (1951) birds also learned several specific numerosities within this range, for instance matching the number of dots on a card to the number of food items to be taken. However, in all the cases just reviewed, considerable amounts of training were required, consistent with Davis and Memmott's (1982, 547) conclusion that "Counting behavior appears to be a relatively unnatural response in infrahumans, and its acquisition may reflect the boundaries of the animal's associative abilities." But about a decade later, Gallistel (1993) suggested that on the contrary "the common laboratory animals order, add, subtract, multiply, and divide representatives of numerosity. . . . Their ability to do so is not surprising if number is taken as a mental primitive . . . rather than something abstracted by the brain from sense data only with difficulty and long experience." One reason for the difference between these conclusions is that Davis and Memmott focused on explicit counting-like behavior, whereas Gallistel was impressed by natural behaviors implying that animals represent numbers of things and perform mental operations on these representations, for example when discriminating between rates of reinforcement or prey capture. In any case, in nature it is often important to give a bigger response to things that are more numerous because these are likely to be indicative of more food, a more dangerous enemy, a hungrier baby, or a more enthusiastic mate. Sometimes it may be important to discriminate specific small numbers of things (Box 10.1). The capacity for such *numerosity discriminations* does not necessarily mean that an animal can be trained to make arbitrary responses to different numbers of items, but it may be more fundamental and phylogenetically widespread.

Accordingly, much of the new wave of research has focused on numerosity discrimination and the representations underlying it. Under some conditions, the numerosity of small sets, up to three or four items, is represented by a precise small number system based on visual object tracking, that is, identification of separate objects as such. Larger numerosities are represented imprecisely in a

Box 10.1 Numbers in the Wild

There are some provocative examples of animals apparently responding to specific small numbers of things in naturalistic contexts, perhaps using the precise small number system discussed in Section 10.2. One such context is nest parasitism, that is, birds laying their eggs in the eggs of another individual (a host) of the same or a different species. For example, the best nests for a cowbird to leave her eggs in are those of hosts that have begun laying but not yet finished. This will ensure that the host starts incubating soon but will carry out the full cycle of incubation needed by the cowbird's eggs. Accordingly, when captive cowbirds are presented with artificial nests holding different numbers, sizes, and/or colors of eggs, they spend more time near and lay more eggs in nests with three versus one "host" egg. This is apparently not sheer preference for more "egg stuff" since they prefer three medium to three large eggs and show little preference when the alternatives are six versus three eggs (White et al. 2007).

Numerosity discrimination may be important to parasites' victims as well. American coot females are sometimes parasitized by other coots and do not eject the parasites' eggs from the nest until after laying has finished. However, because coots use the number of eggs in the nest as a cue as to whether to lay more, it is important to discriminate one's own eggs from others.' Coots which do discriminate others' eggs from their own and eventually reject them lay larger clutches than those which do not (Lyon 2003). The nondiscriminators apparently stop laying prematurely because they count the parasite's eggs as their own.

Another natural context for discriminating small numerosities is in responding to species-typical vocalizations. Crows identify other individuals by the number of their caws (N. Thompson 1969). Chickadees' alarm calls contain more "dee" notes the more dangerous the predator they have sighted (Templeton, Greene, and Davis 2005), and listeners respond appropriately, whether they are conspecifics or other small birds in the neighborhood (Templeton and Greene 2007).

Using auditory cues to number of other individuals might be common among social species because responses to rival groups should depend on numbers of companions and rivals present. For example, when lions hear another pride roaring, they should decide whether to respond aggressively or to retreat from the perceived threat by comparing the number of individuals roaring to the number in their own group (McComb, Packer, and Pusey 1994). McComb and her collaborators tested this idea by playing recorded roars from one or three lions to 21 different lion groups. The bigger the group and the smaller the number of individuals heard roaring, the more likely the subjects were to approach the speaker (Figure B10.1). Similarly, the probability and amount of howling shown by a group of black howler monkeys with one,

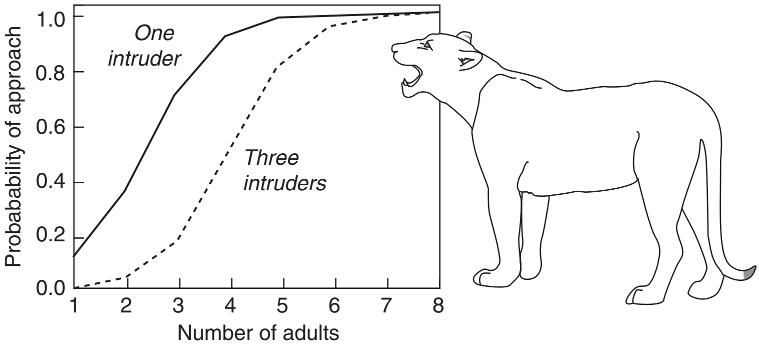


Figure B10.1. Proportion of lionesses approaching a speaker playing recorded roars from another lion pride (simulated intruders) as a function of the number of lions heard roaring and the number in the subjects' pride. Redrawn from McComb, Packer, and Pusey (1994) with permission.

two, or three defenders in response to recorded calls from a group of one, two, or three attackers depends in a graded way on the relationship between the group sizes. This relationship is a measure of the odds that defense will be successful (Kitchen 2004). Finally evidence that a chorus of calls can in fact be unpacked into a representation of a number of individuals comes from a test similar to one conducted with infants (Jordan et al. 2005). Rhesus monkeys heard a recording of two or three conspecifics calling while they looked at two images, one with two vocalizing monkeys and one with three. They looked more at the one showing the correct number of animals, suggesting they have an amodal representation of (at least) small numbers.

way described by Weber's Law in that the discriminability of two numerosities is proportional to their ratio rather than their absolute difference. This implies that a given absolute difference in numerosity between two sets is discriminated more readily if the sets are small than if they are large. As we will see, under many conditions animals (including people) behave as if relying on an underlying continuous representation, or analog, of set size. Accordingly, this system (discussed in Section 10.1) is referred to as the analog magnitude system and that for representing exclusively small numbers as the object tracking system (Section 10.2). The two nonverbal number systems have characteristic "signatures" (Feigenson, Dehaene, and Spelke 2004): precise discrimination with a limit of three or four for the object tracking system and fuzzy Weber's law-based discrimination among quantities of all sizes for the analog magnitude system. Nonverbal numerical competence also includes ranking multiple sets by numerosity. As discussed in Section 10.3, this seems to be part of a wider ability to reason about relative magnitudes which may not be so species-general as the analog magnitude system. Finally, a few animals and all people who have learned to count can, by definition, label quantities precisely with words or symbols. A key question in the comparative and developmental study of numerical competence is the extent to which human verbal counting and other mathematical abilities are built on the nonverbal systems shared with other species (Section 10.4).

10.1 Numerosity discrimination and the analog magnitude system

10.1.1 Discriminating numbers of stimuli

In nature, it must be rare for numerosity as such to vary by itself. For example, more objects occupy more space or take longer to view. More numerous visual objects typically cover more total area and have a longer total edge, or contour length. If more numerous objects are squeezed together in time or space, the gaps between them are smaller than for less numerous ones. Thus a ubiquitous challenge in tests of numerosity discrimination is to disentangle control by numbers of things from control by all the other dimensions of stimuli that usually covary with number. One way to deal with this problem is to acknowledge that number is inevitably confounded with other features and to test for control by number along with control by other potentially relevant features. An example is a test of numerosity discrimination in rats using a procedure essentially the same as the bisection procedure for temporal discrimination described in Chapter 9 (Meck and Church 1983). Responses on one lever were reinforced following two 1-second pulses of tone; responses on a second lever were reinforced after eight pulses (Figure 10.2). Thus, in this stage of training the total duration of the pulse train was perfectly correlated with number of pulses. Once the rats were performing accurately, they had two types of unreinforced test trials. In tests for control by number, the total duration of the stimulus was constant at four seconds and the number of tone pulses varied between two and eight. In tests for control by duration, there were always four tone pulses but the duration of the four tone on–tone off cycles varied between two and eight seconds. The rats' discrimination proved to be controlled by both time and number: their tendency to choose the "long/many" lever (i.e., the one that was correct after 8 pulses/8 seconds) increased with either the duration or the number of tone pulses, as shown in Figure 10.2. Notice that the number at which "two" and "eight" are chosen equally often, that is, the number perceived as halfway between 2 and 8, is not 5 but 4. That is, the numerosity continuum, like the temporal continuum, is bisected at the geometric rather than the arithmetic mean, consistent with Weber's Law.

Data from pigeons show a similar pattern (Emmerton 2001). In a particularly elegant example, pigeons discriminated "many" versus "few" dots in a visual display with a wide range of numerosity pairs (Emmerton and Renner 2006). However, when flashes of light were the stimuli, unlike rats, pigeons were more influenced by time than by number (W. Roberts and Mitchell 1994). Control by number increased relative to control by time when the birds were trained for several sessions with number relevant and time irrelevant. These results, like those from rats, suggest that time and number are processed simultaneously, in parallel. W. Roberts and Mitchell (1994) provided further evidence for this conclusion by training pigeons to use the colors of the choice keys as instructions whether to report the duration or number of the just-presented flashes. The birds learned to respond appropriately even on trials when time and number dictated competing choices. They must have been processing time and number on every trial because the colored choice keys appeared only after the last flash of light. Data like these suggested a model of counting successive stimuli consisting of the information processing model of timing (Figure 9.10) with an added channel for accumulating counts and comparing them with the contents of a reference memory for counts (W. Roberts and Mitchell 1994). If animals

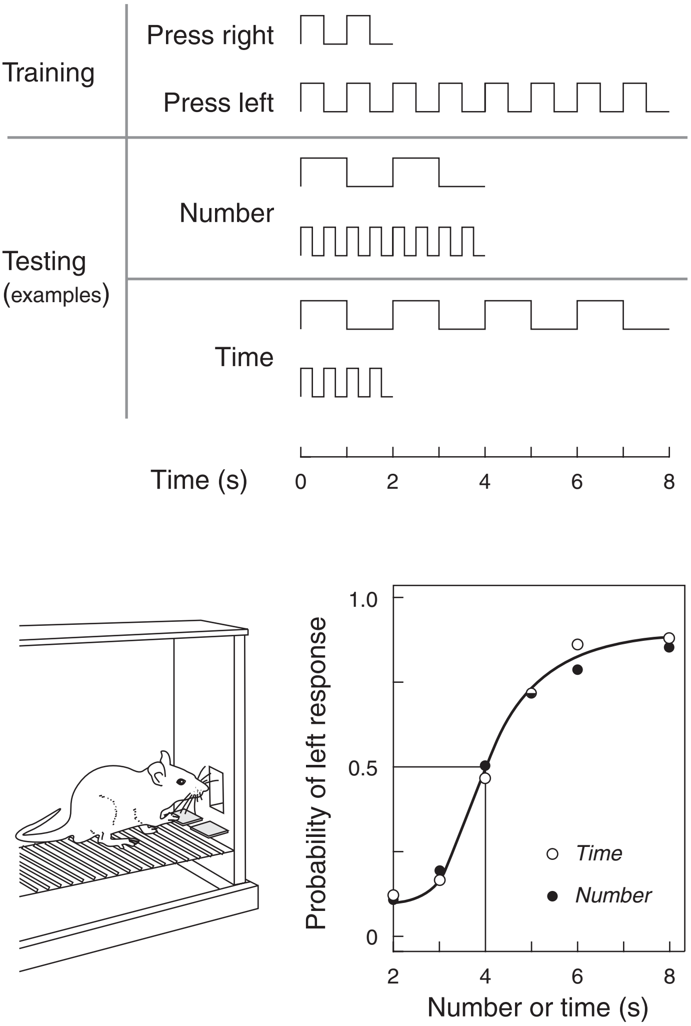


Figure 10.2. Procedure and results demonstrating joint control of rats' choices by duration and number of tone pulses. Data from Meck and Church (1983) with permission.

respond to rates of events by in some sense mentally dividing numbers by times, as in rate expectancy theory (Chapter 4), both channels must be operating all the time.

Further features of the analog magnitude system were documented by Jordan and Brannon (2006) with rhesus macaques, again starting with anchor values of two and eight. The monkeys learned to match samples of two or eight dots to stimuli that matched in number but differed in size, distribution, density, and/or total surface area of the elements. For example, after a sample of two large dots, the monkeys might have to choose two small dots over eight small dots whose total area matched that of the sample dots. Once they were performing well, the monkeys were tested in the typical bisection procedure, with choice between two and eight following samples of intermediate values. As with the rats and pigeons, 50:50 choice occurred nearer 4 than 5. Bisection was again reasonably near the predicted value when the monkeys were further trained with samples of three and twelve. In the final stage of this study, samples had any number of dots from 1 to 9, and the variable of interest was the ratio between the numerosities of the correct match and the distractor. Again in accord with Weber's Law, accuracy and reaction time were predicted by the ratio between the match and the distractor, not their absolute difference. For example, performance was about the same with a sample of 2 and distractor of 4 as with a sample of 4 and a distractor of 8.

10.1.2 Counting responses

Animals also discriminate the numbers of their own responses in a way described by the analog magnitude system. For example, a number of responses on a central key or lever presents two side keys or levers, and the animal is reinforced for choosing the left after one number of responses and the right after a different number of responses. Just as with stimuli, both time and number matter in discriminations of response numerosity and the results obey Weber's Law (Fetterman 1993). Weber's Law implies that greater numerosities are detected with proportionately greater variance. A nice example comes from parallel studies of response counting by rats and humans (Figure 10.3). (Note that number and duration were somewhat confounded here, but related studies have separated number from duration, as discussed by Davis and Memmott 1982). Platt and Johnson (1971) trained rats on what was essentially a *fixed ratio schedule* (i.e., reinforcement was given when the rat had made a fixed number of responses), but when the ratio requirement had been met, the rat had to leave off lever-pressing and put its head into the food tray. If the rat had completed at least the required number of presses, food was given followed by a 10-second timeout with the light off and the lever retracted before the next opportunity to complete the ratio. Premature tray entries started the timeout and restarted the ratio. With requirements from 4 to 24 presses, the probability of a tray entry after different numbers of presses described a set of distributions beautifully in accord with Weber's Law (Figure 10.3), with standard error proportional to the mean. Whalen, Gallistel, and Gelman (1999) obtained similar data from people (Figure 10.3, bottom) by telling them to press a computer key as fast as they could to a target number of presses that varied from trial to trial between 7 and 25. Evidence that the speed requirement encouraged nonverbal counting came from trials showing that fast silent counting to a given target number above about 12 took substantially longer than pressing the key the same number of times. Evidence that subjects were not primarily timing their presses rather than counting came from the fact that timing judgments within the same setting were much more variable than judgments of numbers of presses. The response-counting task, along with a parallel flash-counting task in the same study, therefore seems to tap the same nonverbal analog magnitude system evident in nonhuman species.

10.1.3 Spontaneous numerosity discrimination

None of the studies described so far addresses whether animals spontaneously encode numerosity as Gallistel (1990) suggested because they all involved extensive training. However, at least for some settings and species, numerosity is a more salient aspect of visual stimuli than some other features. Cantlon and Brannon (2007) trained rhesus monkeys in a matching to sample procedure similar to that used by Jordan and Brannon (2006) except that the alternatives in the choice phase always differed in number and in color, shape, or surface area. The correct option matched the sample in both features. For

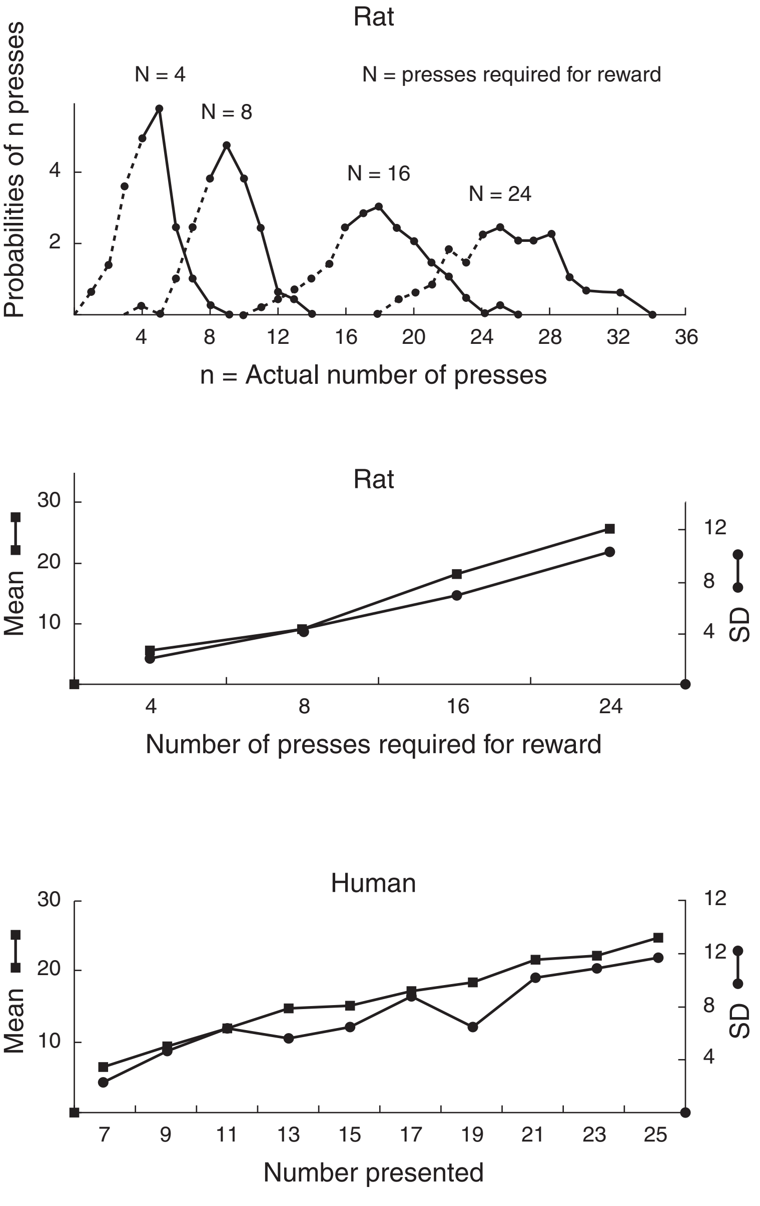


Figure 10.3. Top. Data from separate groups of rats trained by Platt and Johnson (1971) to press a lever N times before switching to a second response, shown as the proportions of trials with different actual numbers of presses. In the middle panel the same data are replotted as mean and standard deviation to show they are correlated as predicted by Weber's Law. The bottom panel shows data of a typical human in a comparable test of nonverbal counting, described in the text. Redrawn from Platt and Johnson (1971) and Whalen, Gallistel, and Gelman (1999) with permission.

example, with a sample of three red stars, the choices might be three red stars and five green stars. Number was placed in conflict with one of the other features in probe trials. For instance, in the example just given, color could be placed in conflict with number by presenting a choice between three green stars and five red stars. With numerosities up to eight, monkeys tended to choose on the basis of numerosity, and accuracies depended on the ratio of sample:distractor numerosities as Weber's Law predicts. The other features did have some effect, however, especially with sample:distractor ratios close to 1 and more so in one monkey without previous numerosity training.

Clearer evidence for spontaneous encoding of numerosity comes from habituation-dishabituation studies with monkeys (cotton-top tamarins; Hauser et al. 2003) and babies (Lipton and Spelke 2003) using auditory stimuli. Subjects were habituated to trains with a fixed number of sounds, syllables from human speech for the tamarins and brief natural sounds for the babies. Trains of different durations but a fixed number of various sounds were presented during the habituation phase, to ensure that habituation was to number and not some other variable such as total duration or sound energy of the train. Orienting to the speaker was then compared for novel trains with the same or a different number of sounds. As shown in Figure 10.4, the study with tamarins explicitly tested for the approximate large number system by including trials with habituation to numerosities of 4 and 8 followed by tests designed to discriminate responding based on absolute or relative difference. The tamarins were sensitive to a 2:3 ratio (i.e., 4 vs. 6 and 8 vs. 12) but not a 4:5 ratio even when, in the case of 8 versus 10, this involved an absolute difference in numerosity that they detected in the 4 versus 6 discrimination.

The precision of babies' discrimination increased with age. Six-month-olds habituated to trains of eight sounds dishabituated to trains of 16 but not 12 sounds, whereas nine-month-olds given the same treatment dishabituated to 12 but not 10 sounds. The consistency of these ratios across absolute number was not tested, but it was tested in a comparable study using visual displays (Xu and Spelke 2000; see also Xu, Spelke, and Goddard 2005). In that experiment, 6-month-olds discriminated 16 from 8 items, and 32 from 16 items, the same 2:1 ratio needed for auditory stimuli in Lipton and Spelke's (2003) study. In comparable tests, adults discriminate ratios down to 1.15:1 (see Feigenson, Dehaene, and Spelke 2004), but they still show the ratio signature of the analog magnitude system. However, the conclusion that these habituation studies all demonstrate sensitivity to number per se is controversial (Mix,

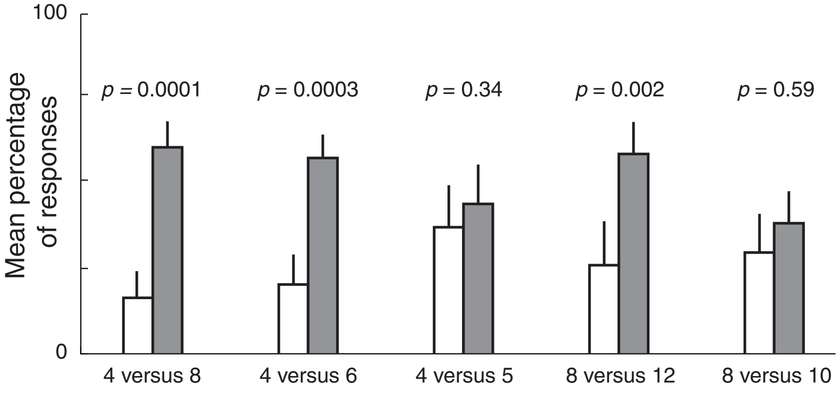


Figure 10.4. Proportion of test trials in which tamarins oriented to the sound train with the same number of elements as in habituation (white bars) and to the train with a novel number, as a function of the contrast between them. Adapted from Hauser et al. (2003).

Huttenlocher, and Levine 2002). Among other problems, continuous variables may not always have been controlled well enough, and when they are, number sometimes turns out to be of no importance. A reasonable conclusion (Hurewitz, Gelman, and Schnitzer 2006) and one consistent with data from other paradigms already presented here is that both number *and* continuous variables are processed but that which is attended to or most important depends on the circumstances. Even when human adults make quick comparisons of the numbers of dots in two displays, they make more errors when number conflicts with size of dots, as when 4 big dots are contrasted with 8 little ones (Hurewitz., Gelman, and Schnitzer 2006).

Another way to test spontaneous numerical representations is to let the subject watch while items of food are hidden in one or more containers. The subject, generally a monkey or baby, then shows how much food it expects by where and/or how long it searches. In one such study (K. Lewis, Jaffe, and Brannon 2005) mongoose lemurs (*Eulemur mongoz,* a species of prosiminian, that is, on a different branch of the primate evolutionary tree than monkeys and apes) saw grapes placed one by one into a bucket. The bucket had a false bottom that allowed some the grapes to be placed out of the lemur's reach. For a given number that could be retrieved, the lemurs did indeed search longer after retrieving the last grape when they should have expected to find more, but only when as many as half the grapes deposited were unavailable. Thus at ratios of 1:2, 2:4, and 4:8 they increased searching with missing grapes, but not for 2:3 or 3:4. Notice that the ratio limit to discriminability indicates that only the analog magnitude system was called into play, even though some experiments to be described in Section 10.2 indicate that numbers as small as 3 or 4 may be represented with the precise object tracking system.

10.1.4 The analog magnitude scale

The top panel of Figure 10.3 suggests that the analog magnitude representation is linear with number in that equal numerical intervals are shown as equal intervals on the x-axis. Linearity is consistent with the notion (e.g., W. Roberts and Mitchell 1994) that counting is accomplished by the same accumulator system as timing, since Chapter 9 suggested that time is perceived linearly with real time but with scalar variance. Indeed initial discussions of the analog magnitude system suggested that it reflects an accumulator-like mechanism, that is, a process of implicit enumeration, but more recent discussions (e.g., Feigenson., Dehaene, and Spelke 2004) simply assume a monotonically increasing linear or logarithmic representation of set size, as in the visualizations in Figure 10.5. The many data supporting Weber's law for numerosity are equally consistent with this representation being logarithmic with constant variance as with its being linear (Figure 10.5). On the whole, behavioral data cannot discriminate between these mathematically equivalent formulations. However, neurobiological data are more consistent with a logarithmic scale (Nieder 2005). These come from monkeys trained in a matching to sample task in which they have to hold in mind the number of dots in a sample and choose the display with the matching numerosity at test. Single cells in the prefrontal cortex recorded during the delay fire selectively for specific numerosities between one and five, but with tuning curves that are symmetrical on a logarithmic scale (see also Nieder, Diester, and Tudusciuc 2006). Numerosity of simultaneously present items may in fact be perceived directly by the visual system, at least in humans (Burr and Ross 2008).

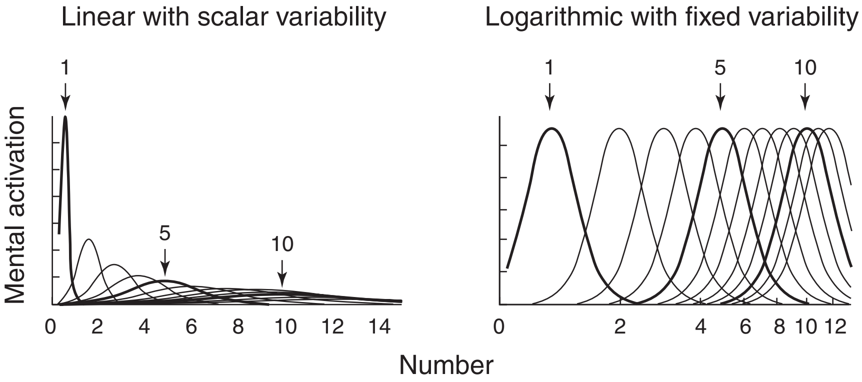


Figure 10.5. Two possible representations of the analogue magnitude scale. Numerical discrimination based on either of these representations obeys Weber's Law. Redrawn from Feigenson, Dehaene, and Spelke (2004).

One study of response number discrimination by pigeons also provides evidence more consistent with a logarithmic than a linear scale (W. Roberts 2005). The pigeons were trained in a typical bisection procedure to discriminate 1 versus 8 or 2 versus 16 pecks. The normal association of number of pecks with time spent pecking was disrupted by presenting the response key briefly at irregular very short intervals to allow only one peck at a time. Tests with intermediate numbers gave the expected result of bisection at the geometric mean. The birds were then trained, in effect, to bisect the interval between smallest and largest number at its arithmetic mean by reinforcing one choice following numbers below the mean and the other following numbers above it. Like the original bisection data, the resulting data were much better fit by a model assuming logarithmic rather than linear scaling.

10.2 The object tracking system

10.2.1 Signature limits

Several hundred rhesus macaques, a species not native to the New World, live and breed in a semi–free ranging state on Cayo Santiago, a small island off Puerto Rico. Because they are habituated to human activities, the monkeys approach and watch when people do interesting things with food. In the study with results depicted in Figure 10.6 (Hauser, Carey, and Hauser 2000) individual monkeys each watched on a single occasion as apple slices were placed one at a time into each of two boxes. Whether the larger number was deposited in the first or the second box, on the left or on the right, by one experimenter or another, was all equated within each condition. When both experimenters had finished hiding food, they retreated and allowed the monkey to approach one box. As the figure shows, the box with the larger number of slices was chosen only when neither number was greater than 4. Notice that ratio does not matter here, nor does absolute difference: monkeys chose the greater number with 2:1, 3:2, and 4:3, but chose randomly with 8:4 and 8:6. A second experiment in which rocks accompanied the smaller number of apple slices showed that the monkeys responded to pieces of food as such, not some other feature like time taken to place

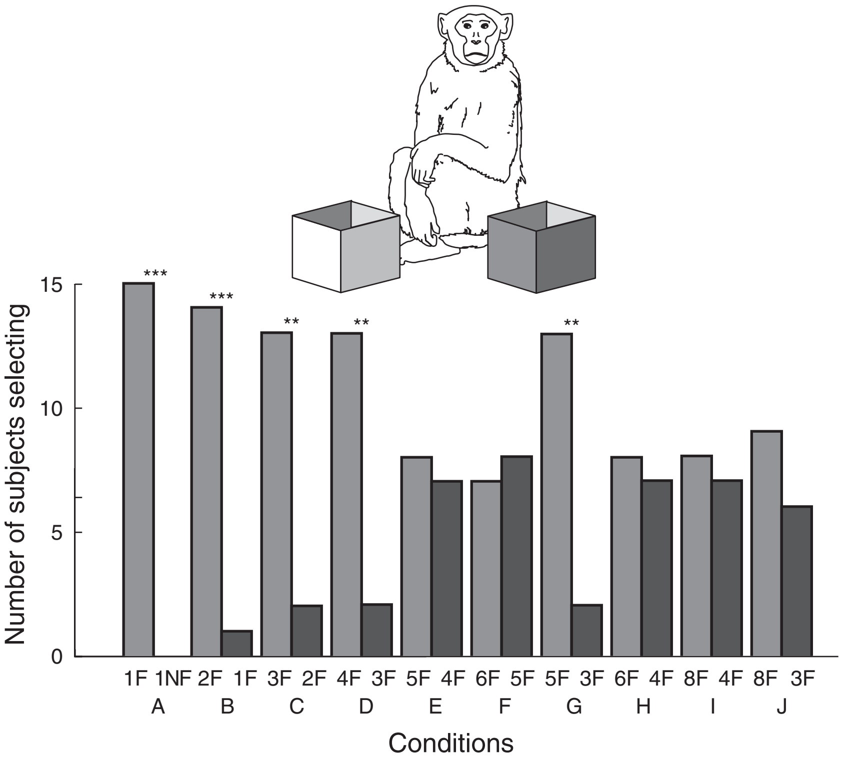


Figure 10.6. Results of Hauser, Carey, and Hauser's (2000) study of free-ranging rhesus macaques, showing number of monkeys out of each group of 15 animals selecting the box in which the given number of items had been deposited. F = food; NF = a non food item, a rock. As noted in the text other researchers have found no preference for 5 over 3 items (Condition G). Light gray = larger number of items; ** = statistically significant difference. Adapted from Hauser, Carey, and Hauser (2000)

items in the boxes. For example, they chose 4 apple slices over 3 apple slices and a rock. In a further experiment replicating aspects of this one (Barner et al. 2008), monkeys showed no preference in either 2:5 or 3:5 conditions, consistent with the conclusion that the system of numerical representation involved here has a set size limit of 4 in adult macaques. However, Barner and colleagues did find a preference in a 1:5 condition, consistent with other data within their study indicating that under some conditions monkeys' choices reflect not a precise representation of set size but a representation of "some" versus "one" (or "none"). The latter kind of representation is especially favored when items are presented as a united set, that is, placed in a container all together on a tray rather than one at a time.

In an adaptation of Hauser, Carey, and Hauser's (2000) method for babies, 10- to 12-month-old infants watched graham crackers being put into two opaque buckets (Feigenson, Carey, and Hauser 2002). About 80% of babies approached the bucket with the greater number for 1:2 and 2:3 but only about 50% did so with 3:4 or even 3:6. Several control conditions indicated that the failures at larger numbers were not due to the greater duration and/or complexity of activity the infants needed to remember. In this paradigm, total amount of cracker was sometimes more important than total number: two regular-sized crackers were rejected in favor of a single very large cracker, and chosen equally with a single double-sized one. Representations of small numbers of individuals as such were perhaps more clearly revealed in a study of searching time (Feigenson and Carey 2005) similar to that with lemurs reviewed in Section 10.1.3 (K. Lewis, Jaffe, and Brannon 2005). Year-old babies watched as balls were placed into a box and were then allowed to search for them. For example, babies that should have expected 3 balls but got only 2 because one was surreptitiously removed were compared to babies that saw 2 balls hidden in how long they spent reaching into the box after finding the second ball. The former group searched longer, revealing discrimination of 2 from 3. Remarkably, both when searching and in a choice test, babies failed a test of 1 versus 4 even though the total number of items to be represented is the same as in 2 versus 3, and both ratio and absolute difference should favor success in 1 versus 4. Like Barner and colleagues (2008), however, Feigenson and Carey (2005) found evidence that sets too large for the object tracking system can still be represented as "some."

10.2.2 Babies and monkeys do arithmetic

Some of the babies' and monkeys' choices in the studies just described may seem paradoxical, but at first glance the results of a series of looking time studies with small numbers of objects are even more remarkable. Figures 10.7 and 10.8 show data from experiments in which 5- to 6-month-old human infants (Wynn 1995) and wild rhesus monkeys (Hauser, MacNeilage, and Ware 1996) watched as objects were placed behind a screen, and their looking time was measured when the screen was removed. For both species, a small number of habituation trials with possible displays or with displays involving no change in numbers of objects (see Figure 10.8) was followed by a test in which responses to possible and impossible displays could be compared across groups. Looking time on various sorts of control trials was measured to assess the possibility that subjects simply look longer at certain static displays, for instance

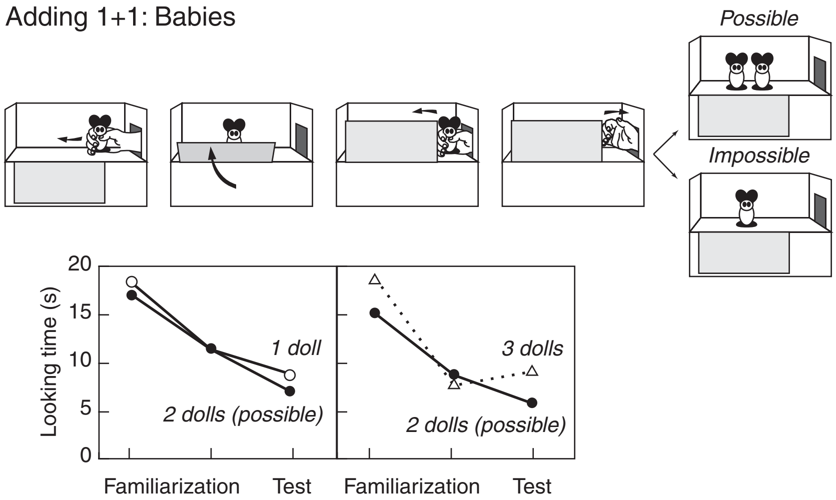


Figure 10.7. "Arithmetic" in infants. Babies sat in an infant seat watching the "puppet show"; in the familiarization phase they were exposed to the individual events later presented in these tests. Redrawn from K. Wynn (1992, 1995) with permission.

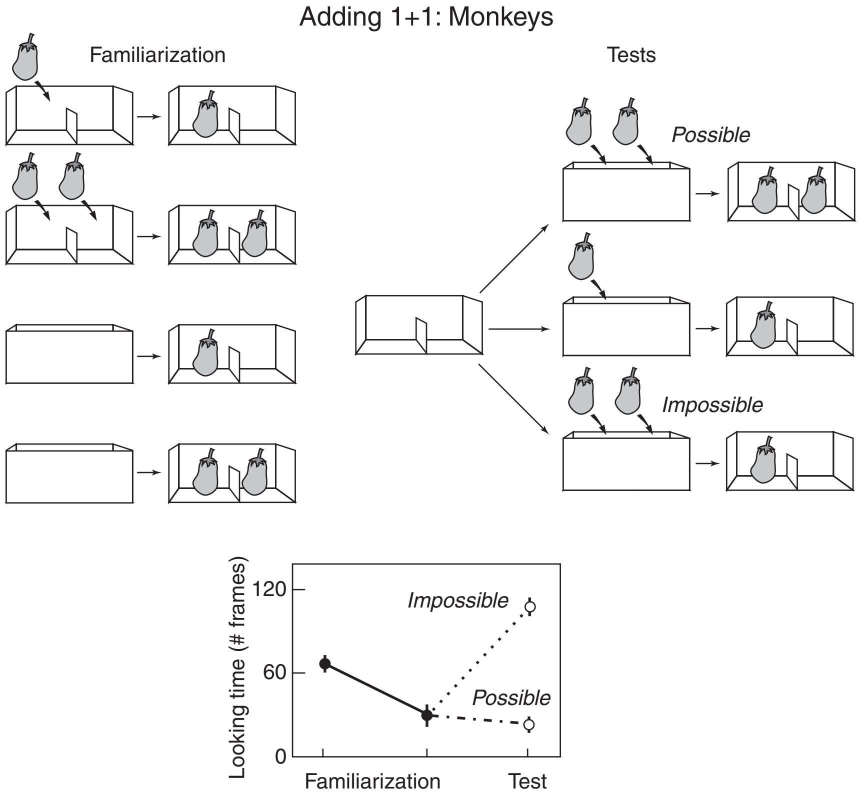


Figure 10.8. "Arithmetic" in free-ranging rhesus macaques. The objects were purple eggplants. Familiarization involved exposure to two of the four sequences on the left. As in Figure 10.7, looking times (measured here in film frames) were scored by observers unaware of which condition the subject was viewing. Redrawn from Hauser, MacNeilage, and Ware (1996) with permission.

those containing more objects. They looked longer at a numerically impossible display such as one corresponding to "1 + 1 = 1," than at a possible one such as "1 + 1 = 2," as if mentally adding and subtracting as objects were inserted or removed from behind the screen (see Wynn 1992). However, the fact that changes in the displays must take place rather quickly (cf. Hauser., MacNeilage, and Ware 1996; Hauser and Carey 1998) is more consistent with the idea that they are tracking a temporary perceptual representation, as discussed in the next section.

As suggested by the examples in Figures 10.7 and 10.8, the original studies of "arithmetic" did not dissociate amount from number. The monkeys, for example, could have been tracking total amount of "eggplant stuff" behind the screen. At least in the case of "1+1," number is more important to the monkeys than total amount: after two small eggplants had been placed behind the screen, monkeys that saw a single large one revealed looked longer than animals that saw the possible outcome of two small ones (Hauser and Carey 2003). However, as discussed in Section 10.1.3, the notion that babies are responding to number as such in looking-time studies is controversial (Mix, Huttenlocher, and Levine 2002). Indeed, in some studies with a "1+1" event like that depicted in Figure 10.7, infants look no more when one big doll emerges from behind the screen than when two small ones do (Mix, Huttenlocher, and Levine 2002). If multiple features of visual objects are encoded in working memory, their relative importance might be expected to vary, just as it does when larger numbers are involved (Hurewitz, Gelman, and Schnitzer 2006). When other features are controlled, infants may fail to respond to small numerosities while continuing to respond to larger ones, perhaps further evidence for two distinct systems (Xu, Spelke, and Goddard 2005). In any case, the conditions necessary to bring out "arithmetic" in these situations are not yet entirely understood. For example, when objects were initially presented as a set (e.g., four lemons in a row) in an experiment like Hauser and Carey's (2003), wild rhesus macaques looked longer at possible than at impossible outcomes with totals up to 4 + 4 (Flombaum, Junge, and Hauser 2005). With size of item controlled, discrimination was based on ratios of set sizes. As another exception, when chimpanzees watched banana pieces placed into two containers one at a time over a period of up to 20 minutes, they reliably chose the container with the greater number at totals up to 6 versus 10 (Beran and Beran 2004). In this study, items were not placed first into one container and then into another, but in a mixed order, and the location of neither the first nor the last item predicted the animals' choices.

10.2.3 What is going on?

Tests of monkeys and babies which reveal small set size limits for numerosity discrimination do not tap numerical representation as such but rather short term memory for visual objects (Feigenson, Dehaene, and Spelke 2004; Barner et al. 2008). A large body of data on human visual attention and memory indicates that objects appearing in the visual field are "tagged" with a spatio-temporal address linking their features into a unified object or "object file" (see Chapter 3), a process also referred to as *parallel individuation* (Barner et al. 2008). Human adults' working memory capacity is 3 or 4 such items (Luck and Vogel 1997), the same size as the implicit representations of set size in monkeys and babies. On this view, in demonstrations of "arithmetic" or searching for missing objects the subject is revealing how it encoded the number of items in a single set by looking or searching longer when the outcome does not match expectation. In choice experiments, two sets are compared not in terms of magnitude as such but in terms of one-to-one correspondence between members of the sets. The larger is the one with, as it were, leftover items. On this interpretation the observed set size limits of 3 for babies and 4 for adult macaques is a limit on items per set, not total items in working memory. Thus babies "pass" with 2 versus 3 but fail 1 versus 4 even though each comparison involves 5 items altogether (Feigenson and Carey 2005). Once one set exceeds the limit for object files, one-to-one correspondence is no longer possible, even though the larger set may still be represented as "some," and chosen over none or one (Barner et al. 2008). Note too that because object files encode multiple features of objects, changes in size or type of objects as well as their number may also increase looking time, and it may be difficult to predict which features will be important (Hurewitz, Gelman, and Schnitzer 2006).

Particularly in earlier discussions of animal numerical competence, discriminating numbers of items in very small arrays has been attributed to *subitizing*, apprehending the number of things in an array immediately, without counting, perhaps by recognizing the distinctive patterns formed by 1, 2, 3, and so on, objects (e.g., Starkey and Cooper 1980; Davis and Perusse 1988). Not everyone agrees that there is a distinct subitizing process (e.g., Gallistel 1990; D. Miller 1993), but if there is it would be used with simultaneously presented arrays of small numbers of items, like those that can be labeled by highly trained animals as described earlier in the chapter. For example, three objects can be arranged on a flat surface in only so many ways, and in its extensive training to identify examples of "three," H. Davis's (1984) raccoon may have memorized most of them.

10.2.4 When is object tracking used?

We have seen evidence for two ways of representing numerosity, each with its distinct signature. In the analog magnitude system, numerosities of unlimited size are discriminated in the fuzzy way described by Weber's Law. In the object tracking system, small numerosities are represented precisely, up to a limit of about 4 for adult humans and macaques and 3 for human infants. Within these small limits, absolute difference matters, not ratio. But object tracking is not the only way of representing small numerosities, that is, it is not *the* "small number system." Under some conditions monkeys or babies simply encode a small set as "some," a quantity greater than one or zero (Barner et al. 2008). And in many cases, numerosities from 1 upward are encoded in common as analog magnitudes. This means that when a range of numerosities is used within a single task, no discontinuity appears around 3 or 4, and discrimination accuracy is predicted by the ratios of the quantities compared regardless of their sizes. An example is Brannon and Terrace's (1998) operant study with rhesus macaques described in the next section. Initial training with numerosities from 1 to 4 transferred seamlessly to larger numerosities, and the ratio rule described data from all numerosities.

In a revealing example, Beran (2007) gave two rhesus macaques a virtual version of the task in which Hauser, Carey, and Hauser (2000; Hauser and Carey 2003) found evidence for the object tracking system with wild monkeys. Beran's monkeys were very experienced with computerized tasks that they accessed freely from their home cages and performed many times a day. They watched as a hand appeared to release small red squares into two containers at the bottom of the computer screen. Reinforcement was given for moving a cursor to the container with more items. Sets varied in size from 1 to 10 items, with controls for total area of the items and total time taken for them to drop. The monkeys' performance fell uniformly as the ratio of set sizes increased, with no evidence that the object tracking system was being used even when both numerosities were small. Like those of Brannon and her colleagues, these findings suggest that the analog magnitude system is called into play for small magnitudes when animals are very experienced with a task, although it is not yet clear how much experience might be necessary, or why experience should matter in the first place.

10.3 Ordinal comparison: Numerosity, serial position, and transitive inference

10.3.1 Ordering numerosities

As we have seen, pigeons and rats implicitly order numerosities in that their probability of rating novel stimuli as having "many" rather than "few" elements increases smoothly as a function of numerosity. Similarly, pigeons given a choice of two or more stimuli each associated with a different delay or amount of food choose them in order from largest to smallest reinforcer (Olthof and Santi 2007). But human numerical competence includes the ability to order an infinity of magnitudes along the real number line. Such explicit ordination has been studied almost exclusively in rhesus macaques and a few other primates. As we will see, numerical ordination tasks seem to tap a more general ability to represent and reason about things that vary in magnitude, whether numerosity of elements, position in an arbitrary sequence, or ranking in a social hierarchy.

Brannon and Terrace (1998, 2000) demonstrated that rhesus macaques could explicitly order numerosities using a version of the simultaneous chaining task to be discussed further in Section 10.3.2. The monkeys saw exemplars of the numerosities 1–4 simultaneously displayed on a touch-sensitive computer screen, as in Figure 10.9. The locations of the different numerosities changed from trial to trial, and in the final stage of training so did the color, shape, size, arrangement, and so forth, of the items in the displays, ensuring that the monkeys based their responses on numerosity alone. Once they had learned to touch four images in order of increasing numerosity even when the images were novel, test trials began with the numerosities 5–9. In this stage just two images appeared on each trial and touching them in order of increasing numerosity was reinforced only if both were familiar. Otherwise test trials were not reinforced. The monkeys performed far above chance even with novel pairs like 6 versus 8. Over all pairs, accuracy increased and latency to touch the first item decreased with numerical distance. In addition to this *numerical* (or *symbolic*) *distance effect,* they showed a *magnitude effect:* at a constant numerical difference, judgments were quicker and more accurate if the numerosities were small (Brannon and Terrace 2000). Note that Weber's Law implies the magnitude effect, for example, that 3 versus 2 is easier than 9 versus 8.

In initial training with 1 to 4, the monkeys evidently acquired a concept of ordinality or relative magnitude or made use of one they already had. Evidence for the latter possibility comes from an unsuccessful attempt to train one monkey to respond to displays of 1 to 4 items in an arbitrary order (Brannon and Terrace 2000). As we see shortly, monkeys can learn sequences of up to 7 arbitrary images in the same sort of procedure, so this monkey's complete failure with an arbitrary order of

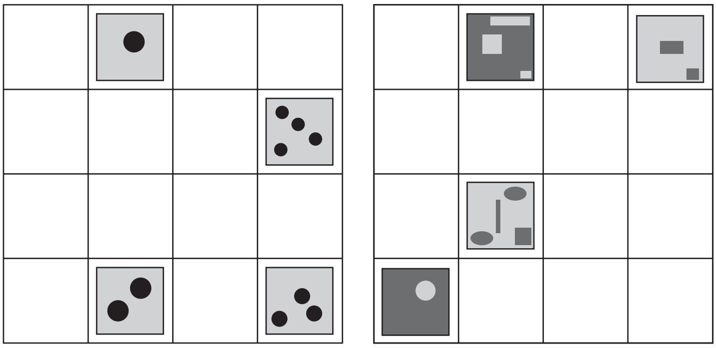


Figure 10.9. Examples of displays used to train macaques to order stimuli by numerosity. The display on the right, with exemplars of the numerosities 1–4 involving items that differ in shape and color, would have been used later in training than the more uniform display on the left. Notice how the locations of specific numerosities in the grid of locations changes from trial to trial. After Brannon and Terrace (2000) with permission.

numerosities (after which he succeeded on the normal order) suggests that monkeys spontaneously not only represent numerosities but order them by magnitude.

In extensions of this work, rhesus macaques transferred ordination skills acquired with numerosities of 1–9 to novel displays with up to 30 items (Cantlon and Brannon 2006). Such monkeys were compared to humans in their ability to order pairs of numerosities between 2 and 30 with controls for nonnumerical features such as density and total surface area of the items. The people were required to answer quickly to discourage counting. As shown in Figure 10.10, monkeys and people showed similar increases in reaction time and decreases in accuracy as the ratio of smaller:larger number approached 1:1. And in a clever adaptation of a human "semantic congruity" task, the same monkeys were trained to use the background color of the touchscreen as a cue whether the smaller or the larger numerosity of a pair between 1 and 9 should be touched first (Cantlon and Brannon 2005). Just like people told to "pick the larger" versus "pick the smaller" of two numerals, at a given numerical distance monkeys were quicker to judge "smaller" than "larger" when both numerosities were small, and quicker to judge "larger" than "smaller" when both were large. Like findings to be described in Section 10.4, these data suggest that human verbal labels for numerosities tap the same nonverbal representation of relative magnitude possessed by other species. As for what those other species might be, information is limited. There has been extensive further work on ordinal judgements with macaques (cf. Terrace 2006) and other primates (Smith, Piel, and Candland 2003; Beran et al. 2005), but little on explicit ordinal judgment of numerosity with nonprimate mammals or birds. The species differences in ranking and reasoning about other magnitude continua reviewed next suggest interesting possibilities for further comparative studies with the paradigm pioneered by Brannon and Terrace.

10.3.2 Ordering arbitrary items: Serial order learning

If arbitrary images replace stimuli related by numerosity, the kind of task depicted in Figure 10.9 becomes a test of *sequence production* or *simultaneous chaining*. The

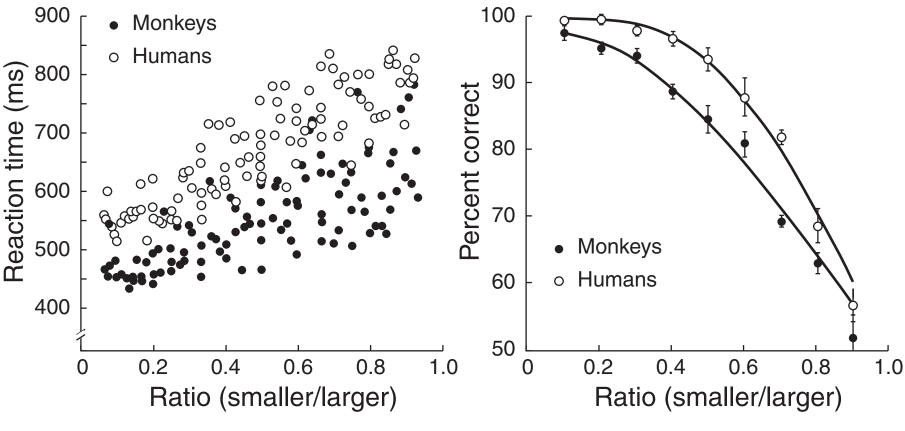


Figure 10.10. Reaction times and proportions of correct responses shown by monkeys and humans touching first the smaller and then the larger of two numerosities as a function of the ratio of the smaller to the larger. Redrawn from Cantlon and Brannon (2006) with permission.

animal's task is to touch or peck five simultaneously presented arbitrary pictures or colors, A–E, in the sequence A–B–C–D–E. Because the stimulus array does not change as the animal responds, it has only self-generated cues to its position in the sequence. And because the spatial arrangement of stimuli changes from trial to trial, the animal cannot memorize a sequence of motor acts. How sequences of responses or stimuli are learned is a classic issue in psychology that touches everything from how rats learn complex mazes to how people learn skills (Terrace 2005, 2006). In principle, such a sequence can be learned without any representation of the sequence as a whole or of items' relative positions within it as such. Animals might acquire a chain of associations so that each item activates a link to the next item in the sequence (Figure 10.11). Pigeons apparently use an even simpler rule. Their performance with subsequences of items such as AB, AC, and CD (reviewed by Terrace 2001) suggests that they learn, "respond first to A, if present, then respond to any other item; if E is present, respond to any other item and then to E." Thus they respond at chance to subsequences like BC that contain only interior items. They also respond equally quickly to the first and to the second items of all subsets, that is, they show nothing analogous to magnitude or distance effects (where magnitude and distance are now defined in terms of position in the sequence.)

Rhesus and cebus monkeys, whose performance in sequence production tasks has been studied extensively (D'Amato and Columbo 1988; Terrace 2001, 2006), behave quite differently from pigeons. They appear to acquire a linear representation of the sequence as a whole, in effect ordered mental slots occupied by specific items (Figure 10.11). Their data from tests with subsets of items parallel those from analogous tests of numerical ordering, as if learning to order unrelated pictures taps the same kind of representation. The latency to respond correctly to the first item increases with its position in the sequence (a magnitude effect), and latency to respond to a given first item decreases as the distance between it and the second item increases (a distance effect). In addition, cebus monkeys (comparable data from rhesus have apparently not been reported) show a "second item effect" (D'Amato and Columbo 1988; Colombo and Frost 2001). The latency to respond correctly to the second item after choosing the first item increases with distance between them (e.g., D is responded to more slowly in AD than in CD tests). On the whole, data from people given the same task show similar patterns (Colombo and Frost 2001). Interestingly, absolute latencies in such experiments as a function of magnitude or distance are substantially longer than those in comparable studies of numerical ordering, perhaps reflecting extra time required to retrieve ordinal information about the arbitrary images (Terrace 2006).

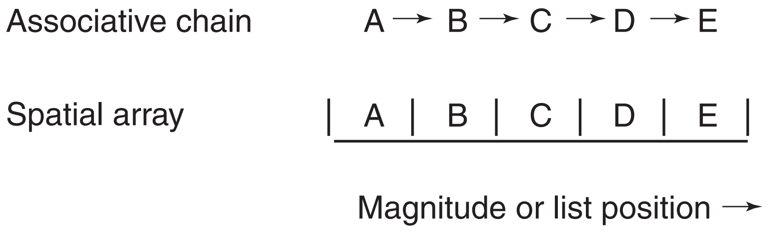


Figure 10.11. Two ways of representing a sequence of actions or events as a function of position: as a chain of associations ("A leads to B leads to C. . . .") or as a linear spatial array.

Of the effects just summarized, the magnitude and second item effects are predicted by learning the list as a chain of associations, since connections should be weaker between items further apart, or further down, in the list. However, the distance effect seems incompatible with an associative representation because it implies that the relative positions of two disparate items are recognized more quickly the further apart they are, as if ordinal position is represented as such. Results of studies in which rhesus monkeys learn multiple lists are consistent with this conclusion. For example they correctly choose first the earlier and then the later item when tested with items from two different lists (Terrace, Son, and Brannon 2003). In one study (Swartz, Chen, and Terrace 1991) monkeys learned four 4-item lists of pictures, A–D, and then had transfer tests in which the familiar items were rearranged to make new lists. They learned the new lists more quickly if the items retained their old relative positions, as for example when A in the new list was A in one of the old lists and it was followed by B from a different old list, and so forth. And monkeys gradually become list-learning experts, learning completely new lists of up to seven items more and more rapidly even when each list is presented in its entirety from the very first trial (Terrace, Son, and Brannon 2003). As Terrace (2006) puts it, this is like figuring out a 7-digit PIN from scratch when the numbers don't even stay put on the keypad. The monkeys' skill implies they have developed a nonverbal strategy for identifying by trial and error first the initial item in the list, then the second, and so on.

10.3.3 Reasoning about quantity: Transitive inference

Nonverbal transitive inference

Transitive inference problems are familiar to every schoolchild. "If Susan is taller than Polly and Polly is taller than Carol, then who is tallest, Susan, Polly, or Carol?" Similarly in animal social life, if A dominates B, and B dominates C, then A probably dominates C. Making such inferences might permit learning one's place without having to fight with everyone in the social group. The functional prediction that follows—that species with a linear dominance hierarchy should be especially successful at transitive inference—has influenced some provocative recent research. However, tests of animals' transitive inference abilities began as tests of "rationality" or "reasoning" based on studies with children using arbitrary stimuli as depicted on the left of Figure 10.12 (McGonigle and Chalmers 1977). The animal learns a set of at least four simultaneous discriminations, construed as forming a series, A>B, B>C, C>D, D>E, where X>Y means that when they appear together X is reinforced and Y is not. Once performing well even when the pair presented varies randomly from trial to trial, the animal is given a choice between the novel pair B and D, each of which has been both reinforced and nonreinforced during training. Not only monkeys (e.g., McGonigle and Chalmers 1977; Treichler, Raghanti, and Van Tilburg 2003) and chimpanzees (Gillan 1981) but also rats (W. Roberts and Phelps 1994; Dusek and Eichenbaum 1997) and pigeons (e.g., von Fersen et al. 1991; Lazareva and Wasserman 2006) reliably choose B over D, but not necessarily for the same reasons. Indeed, the history of research in this area is a good example of how an explanation more or less readily accepted for the performance of primates was deeply (and as it turned out, appropriately) questioned when pigeons showed the same kind of behavior, leading to alternative explanations being devised and tested (Delius and Siemann 1998; Allen 2006).

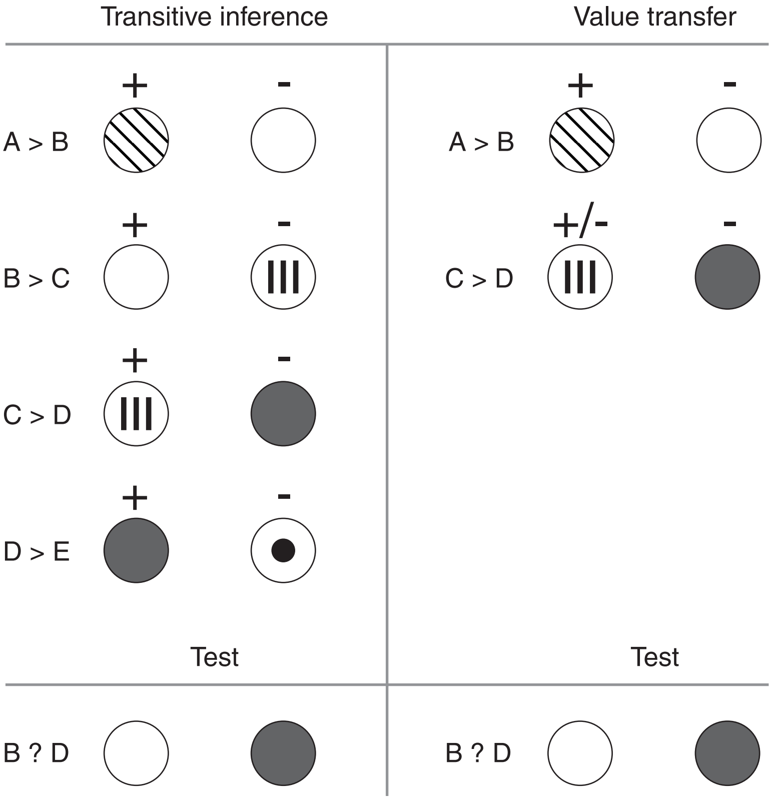


Figure 10.12. Examples of procedures for training and testing pigeons or monkeys in experiments on transitive inference (left side of the figure) or value transfer. The rewarded option in each pair is labeled +.

When people consciously make transitive inferences they seem to rely on a linear, spatial, representation of relative magnitudes; for example, the mind's eye sees Carol, Polly, and Susan standing in order of height. Because other primates seem to use such a linear representation for numerosity and serial order judgements, a reasonable hypothesis is that their transitive inferences rely on a similar representation (Terrace 2005). In addition to correct choice on critical novel pairings, evidence for an overall ordered representation of a series would consist of analogs to the magnitude, distance, and second item effects. A symbolic distance effect has been found in cebus monkeys (D'Amato and Colombo 1990) but as we will see, some such effects are found in other species and may have associative explanations (e.g., Van Elzakker, O'Reily, and Rudy 2003). One effect consistent only with an overall linear representation is inference-like performance when lists are linked, as when one learns the relative speeds of runners in two track teams and then learns that the slowest member of Team 1 outruns the fastest member of Team 2. By analogy, Treichler, Raghanti, and Van Tilburg (2003) taught rhesus monkeys three independent sets of four linked pairs (i.e., involving items A-E, F-J, and K-O) and then linked them by separately teaching "E>F" and " J>K." As a control, either before or afterwards the same monkeys learned three other lists that were not linked. In the experimental condition the monkeys performed substantially better than chance on cross-list pairs from the outset of reinforced testing, whereas in the control condition they began at chance.

Associative explanations of "inference"

Most tests of transitive inference with nonprimates have focused on performance with critical test pairs in a single list, usually B versus D in a 5-item (4-pair) list like that in Figure 10.12. However, there are several ways in which the training procedure might simply give B more associative strength than D. The most subtle arises because, although B and D have similar histories of primary reinforcement, they have appeared in the company of other stimuli with different histories. In particular, B appears not only with C but also with A, which should be very highly valued thanks to never being a negative stimulus in any discrimination in the series. Moreover, D appears sometimes in the company of E, which should be the least-valued stimulus in the series. Thus if B and D gain value by association with the other positive or negative stimuli with which they appear, B should be preferred over D. This sort of indirect acquisition of associative strength is referred to as *value transfer* (von Fersen et al. 1991). Value transfer has been demonstrated directly with the procedure shown on the right of Figure 10.12 (Zentall and Sherburne 1994; Zentall et al. 1996). Pigeons were confronted with negative stimuli, B and D, from two independent simultaneous discriminations, in one of which (A vs. B) the positive stimulus had been reinforced 100% and in the other of which (C vs. D) it had been only partially reinforced. Although both procedures lead to similarly high rates of responding to the reinforced alternative, pigeons reliably pecked more at B than D in the test. However, S+ and S- can interact in more than one way in a simultaneous discrimination (Zentall and Clement 2001), so any preference for B over D remaining despite manipulations designed to equalize value transfer is not conclusive evidence for a linear representation of the series.

Value transfer can be opposed to linear representation by, in effect, bending the linear series on the left of Figure 10.12 around on itself by adding E>A so E and A, together with their associates B and D, no longer have differential value. As value transfer predicts, pigeons did not choose B over D in this "circular" series (von Fersen et al. 1991). However, in an analogous test with rats in which the alternatives were an ordered series of spatial locations, B was still chosen over D, as if the animals had acquired a representation of the relative location of the items in space (Roberts and Phelps 1994). Perhaps this is not surprising when they were ordered in space to begin with; it is not the same as the animal itself generating a spatial representation of inherently nonspatial elements. Overall, tests with circular series have had mixed results (cf. Treichler and Van Tilburg 1996; Delius and Siemann 1998). Consistent with poor performance on a circular series and inconsistent with an overall representation of relationships among items, performance on interior items in a linear series may be strongly influenced by the associative strengths of neighboring items (von Fersen et al. 1991; Van Elzakker, O'Reily, and Rudy 2003). Most unlike what might be expected from pure serial ordering are "end (or anchor) effects": performance is markedly better for the last pair in the series than for interior pairs, reflecting the last item's special status (e.g., Van Elzakker, O'Reily, and Rudy 2003). When monkeys have extensive training in numerical ordering tasks with the same items, an analogous anchor effect becomes one of several determinants of performance (Brannon, Cantlon, and Terrace 2006).

Another line of associative explanation arises from observing that the way animals are typically trained in these tasks leads to reinforcement histories favoring B over D (Wynne 1995; Delius and Siemann 1998). For example, if training starts with "A>B" and successive pairs are added only after the animal meets some criterion on earlier ones in the sequence (as in Bond., Kamil, and Balda 2003), the sheer number of reinforced and nonreinforced choices can vary widely among different items.

Correction trials (Box 6.2) may be used to equate reinforcers to members of a pair, leaving uncontrolled the number of unreinforced choices of each item. A model incorporating this generates transitive choices (Couvillon and Bitterman 1992). Lazareva and Wasserman (2006) tested the dependence of B versus D choices on pigeons' reinforcement history by giving extra D versus E training sufficient to raise each bird's overall ratio of reinforced to nonreinforced first choices of D to a level higher than that for B, but pigeons still chose B on 80% of B versus D tests. Other tests along similar lines, addressed to a variety of associative factors, have had similar results (Wynne 1995; Delius and Siemann 1998). Because there are so many ways in which reinforcement history could produce choices consistent with inference from a linear representation, the basis for any remaining B versus D preference in rats and pigeons is unclear. Tests with lists of more than 5 items (4 pairs) should be most illuminating here because they afford more possibilities for novel pairings of interior items, but even so ambiguities remain. For example, rats trained on a 5-pair series of odors, A-F (Van Elzakker, O'Reily, and Rudy 2003) chose B more often in B versus E than in B versus D tests, but was this a distance effect or did negative value transferred from F reduce choices of E?

Finally, results from studies of "unconscious inference" in human adults show that members of a given species do not necessarily solve transitive inference-like tasks in only one way. Adults have been given a task like that depicted in Figure 10.12, but with Japanese characters. When they are not aware that the pairs form a linked list, their training and test data look much like those of rats and pigeons, but if they are aware of the relationship among the pairs they perform perfectly on all pairs in training and choose correctly in tests with novel pairs (Frank et al. 2005). In a study suggesting that rats may similarly have access to both kinds of representations, Dusek and Eichenbaum (1997) showed that hippocampally lesioned rats could still learn a list of odor pairs but did not perform above chance on B versus D tests whereas intact rats did. They concluded that rats normally rely on a spatial representation of the whole list, but this interpretation is not universally accepted (see Van Elzakker, O'Reily, and Rudy 2003). Moreover, similar effects are not found with pigeons (Strasser, Ehrlinger, and Bingman 2004).

This section of the chapter began with the question whether monkeys and other primates solve transitive inference tasks by reference to the same kind of linear overall representation evident in numerosity and serial ordering tasks. Clearly the associative history of the individual options can generate the choices predicted by transitive inference, but it is still unclear to what extent such factors are actually responsible for monkeys' behavior. We have seen that monkeys solve serial ordering tasks differently from pigeons, but so far the best evidence that the same kind of difference applies in transitive inference tasks is the way in which monkeys respond when separate lists are linked (Treichler, Raghanti, and Van Tilburg 2003), a test not yet reported for other species. In addition, monkeys should be tested with longer lists because these afford the large numbers of interior test pairs necessary for documenting magnitude and distance effects. If transitive inference is an adaptation for a complex social life monkeys and pigeons would be expected to differ just as they differ on sequence production tasks (Section 10.3.2).

Social transitive inference and species differences

Some of the best evidence that transitive inference can be used in social situations comes not from monkeys but from pinyon jays, food-storing corvids that live in stable social groups with linear dominance hierarchies. Paz-y-Mino and colleagues (2004) documented dominance relationships in three groups of captive pinyon jays by observing each pair of birds in a group in a contest over a peanut. Then each experimental bird watched on three occasions as a bird from another group defeated a dominant bird from its own group (Figure 10.13). This experience should have allowed subjects to infer, in effect, "the stranger beats someone who dominates me; therefore the stranger will dominate me." Subjects also saw the same stranger lose a contest with another bird from the stranger's own group on three occasions, thus learning that the stranger could lose as well as win. Control birds saw a stranger both winning and losing contests with others from the stranger's own group, an experience designed to give them no information about their own standing relative to the stranger. And indeed, the first time they encountered the stranger themselves, experimental birds behaved more submissively than controls. Although the effects of observation did not extend beyond the first encounter (and perhaps they should not

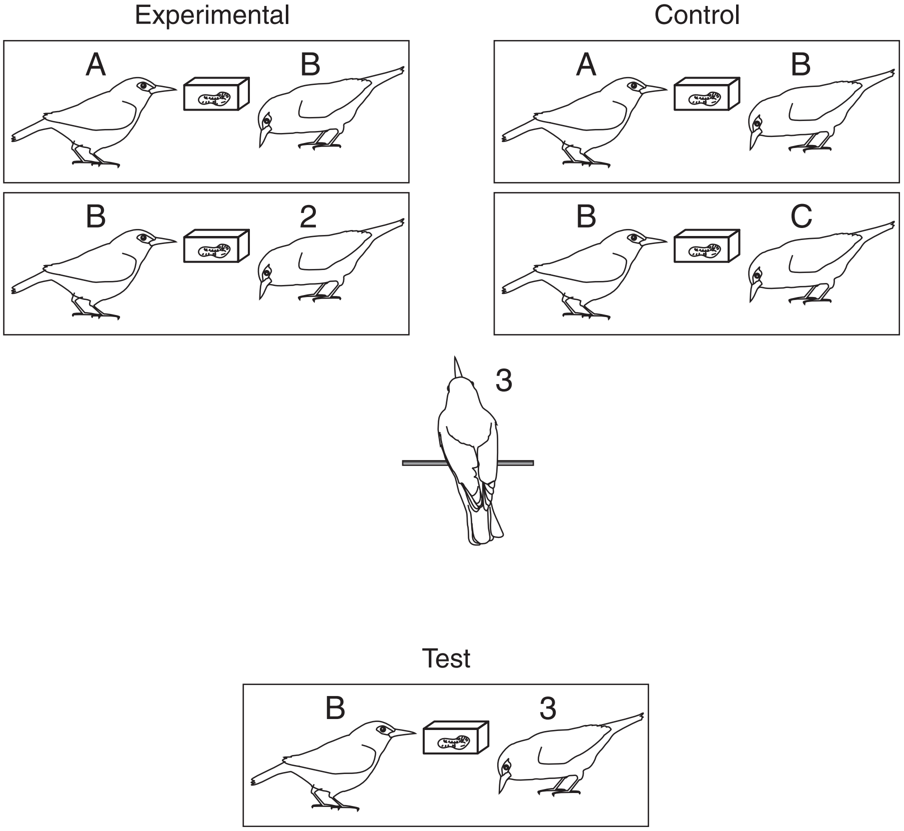


Figure 10.13. Experimental and control conditions in the study of social transitive inference in pinyon jays. Letters and numbers represent birds from two different social groups; relative ranks are represented by their order (e.g., A is dominant to B and 2 to 3). In sketches of the encounters, the bird on the right is behaving submissively to the bird on the left. The box contains a peanut, which would be obtained by the dominant bird. Subjects, here bird 3, watched the encounters like those depicted in the upper part of the figure and were tested as shown. After Paz-y-Mino et al. (2004) with permission.

be expected to), it is noteworthy how quickly the birds appear to have learned the relative rank of the stranger. Also unlike the case in analogous operant tasks, the rankings were learned entirely by observation, without any direct reinforcement of the actions displayed in the test. Hogue and colleagues (Hogue, Beaugrand, and Laguë 1996) showed that hens learn about dominance in a similar way, although with a less well balanced design.

Fish as well as birds and mammals learn about other individuals by watching (Chapter 13). Males of a species of cichlid fish, *Astatolapia burtoni,* were exposed to staged encounters among four pairs of neighbors from which they could infer a whole 5-item hierarchy (Grosenick, Clement, and Fernald 2007). Individual neighbors played different roles in the hierarchy for different subject fish. When then confronted with two of these neighbors, one on either side of a tank, subjects were expected to spend more time near the less dominant member of a pair, and this is what they did, for both the A-E (i.e., most and least dominant) and the B-D pair. Four control fish that witnessed neighbors in a nonhierearchical series of interactions showed no preferences. Again, this learning was very quick. In Chapters 12 and 13 we will see more evidence that bystanders or "eavesdroppers" rapidly acquire information about social relationships.

It is worth wondering to what extent the learning by the jays and fish in these experiments is attributable to the same system involved in the slow and laborious food-rewarded instrumental discriminations that provide the basis for transitive choices in the studies reviewed earlier. One study based on the assumption that the same abilities are involved is a comparison of pinyon jays and scrub jays trained on an operant task with a 7-item (6-pair) list (Bond, Kamil, and Balda 2003). Because pinyon jays live in more complex social groups than do scrub jays, they were expected to learn the task faster and perform more like monkeys on novel tests. The first of these predictions was clearly fulfilled in that even with 100 sessions' extra training the scrub jays never reached the same level of performance as the pinyon jays. Birds of both species were well above chance with novel pairs, but when it came to detailed patterns of performance on interior pairs, the pinyon jays tended to behave more as if they had acquired a linear representation of the series of colors than did the scrub jays. However, the results were not unambiguous. As the authors conclude, the case for species differences here would be strengthened (or not) by further work, for example comparing the two species on list linking.

Stronger evidence that social structure predicts performance on operant transitive inference comes from a comparison of ring-tailed lemurs (*Lemur catta*), a very social species, with less social mongoose lemurs (*Euelmur mongoz;* MacLean, Merritt, and Brannon 2008). Although the two species acquired a task with six pairs equally quickly, the ring-tailed lemurs performed better on tests with novel pairs and showed a clear distance effect not evidenced by the mongoose lemurs (Figure 10.14). Importantly, however, after additional exposure to the training pairs ($A > B, B > C$, etc.) strictly in their sequence in the list, a procedure designed to emphasize their relationship, both species did well equally on novel pairs and showed equivalent distance effects. The authors therefore conclude that the species differ not in transitive inference ability as such but in their predisposition to organize information along a common dimension. How such an ability is related to human domain general ability to reason by transitve inference is open to discussion (see Penn, Holyoak, and Povinelli 2008).

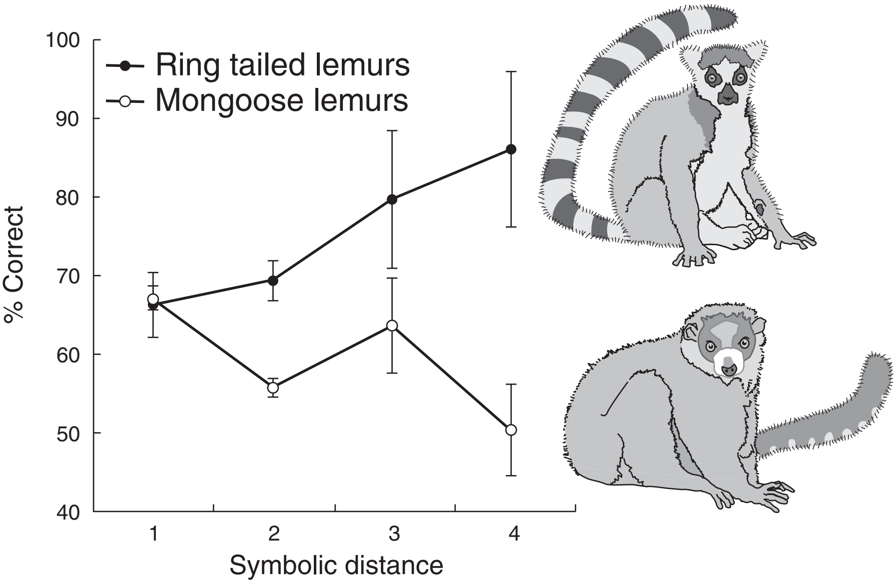


Figure 10.14. Symbolic distance effects compared in two species of lemurs trained on a 7-item transitive inference task. After MacLean, Merritt, and Brannon (2008) with permission.

10.4 Labels and language

We are now back where we began, with animal counting. Given that animals can discriminate numerosities, it is not surprising that a variety of animals can associate specific arbitrary stimuli, including human number words and symbols, with specific numerosities, that is, they can in a sense label numerosities (e.g., Olthof, Iden, and Roberts 1997; Olthof and Roberts 2000; Beran et al. 2005; Olthof and Santi 2007). But does such labeling reveal, or perhaps even convey, any forms of numerical competence that are not evident otherwise? And given that humans and other species share systems for object tracking and numerosity discrimination, is there a special role for counting language in human numerical competence? We address these questions by looking at the uses of number labels by a parrot, a few specially trained chimpanzees and other primates, and people whose language has only a few number words.

10.4.1 Alex the parrot

Alex the African grey parrot was trained for over 20 years to describe his surroundings with English words (Pepperberg 1999). His vocabulary was designed to reveal his ability to categorize objects in terms of features like color, shape, material, and number. After being trained to report the number of items in collections of up to six objects, Alex correctly labeled novel sets of objects on about 80% of trials. He could also say how many objects of a certain type were in a larger array of objects. For example, “How many keys?” on a tray with two keys and four rocks. Like young children, he tended to make errors that consisted of responding with the total number of objects in the array, for example, “six” rather than “two.” When there were two keys among four rocks, Alex might have been subitizing, but not when asked the number of yellow keys in a display containing yellow keys, green keys, yellow rocks, and green rocks. Nevertheless, Alex did respond correctly to more than 80% of such questions (Pepperberg 1994). And like the chimpanzees discussed next, Alex could use numbers to answer questions about addition of small quantities, for example, answering "three" when two items are hidden under one cup and one under another. He also appropriately answered "none" to questions for which "zero items" is the correct answer, although he may not have completely understood the mathematical concept of zero (review in Pepperberg 2006).

A nice demonstration that Alex's number words represent precise quantities followed on from his being taught the names for the Arabic numerals 1 to 6. He learned to name the numerals by rote rather than by pairing them with numbers of things. Having done that he could then correctly answer questions that required identifying the names of the numerals with numerosities. For example, he might be shown a *2* and a *4* of equal size and asked "which bigger?" Or he might see 2 candies and a numeral *3* and be asked "which smaller?" This performance implies that he linked the number symbols to numerosities by way of the common vocalization associated with them, much as in mediated generalization (Chapter 6) and some examples of functional reference (Chapter 14).

10.4.2 Counting chimpanzees

Ai: memory span and planning

Matsuzawa and his colleagues have been studying the cognitive abilities of the chimpanzee Ai for many years (Matsuzawa 2007). Ai learned to match arrays of up to 9 objects by selecting the correct numeral on a touchscreen, but unlike children she did not get any quicker with experience learning new numbers. She also learned to touch numerals in order of magnitude when four or more of them appeared in unpredictable locations on the screen. Typically the longest latency in each chain of responses was to the first item, as if Ai was inspecting all the numerals and planning the required sequence of moves before touching the smallest. This supposition was supported by the finding that when all the remaining numerals were replaced by white squares (i.e., masked) as soon as she touched the first one, she still was able to proceed through the correct sequence on a high proportion of trials, even with five items (Kawai and Matsuzawa 2000). The speed and accuracy with which Ai and other chimpanzees can do the task with masking apparently exceeds that of human subjects (Matsuzawa 2007), but of course the chimpanzees may have had more training. Three other chimpanzees and two monkeys were trained to do essentially the same task by moving a joystick to select numerals up to 5 in order. In addition to masking trials, they were subjected to trials in which the locations of two items were swapped after they had begun the sequence, which again should disrupt a planned series of moves. These animals seemed to plan ahead only to the next move in both numerical and arbitrary sequences of items, possibly because selecting moves with a joystick is more attention demanding than just touching them, leaving fewer cognitive resources for planning (Beran et al. 2004).

Numerals and the reversed contingency task

Sally Boysen and her colleagues trained three chimpanzees to label small collections of objects with Arabic numerals (review in Boysen 1993). Their education began with training on one-to-one correspondance, matching numbers of gumdrops to numbers of tokens stuck on cards. Then cardinal numbers replaced the tokens. Eventually the animals could make appropriate choices of arrays when shown Arabic numerals and vice versa. They could use numbers up to 6 or 8 as well as zero. Finally, one animal, Sheba, was allowed to find up to four oranges in any of three places in a room. She reported what she saw by searching the hiding places and choosing the corresponding numeral. The cards with numerals were placed so that Sheba could not see the experimenter while making her choice (Figure 10.15). When oranges were in more than one place, Sheba correctly reported the total number of oranges, apparently adding the numbers found in different locations. To probe further the extent to which numerals represent numbers of things for the animal, Boysen and Berntson (1989) hid cards with numerals. For instance, a *1* might be hidden in one place and a *3* in another. Having seen two numerals, Sheba correctly reported their total. Most remarkably, Sheba's performance was better than chance from the first encounter with this task.

Two of Boysen and Berntson's (1995) number-trained chimpanzees were the first to be studied in a *reversed-contingency task:* in this task the animal is offered a choice between two quantities of food and receives the one it does *not* indicate. In their original experiments whatever the subject selected was given to another chimpanzee in a facing cage, and the subject had what remained. In nearly 100 trials' exposure to this contingency, Sheba and Sarah persistently pointed to the larger quantity more than 50% of the time, and their tendency to make the "wrong" choice was greater the greater the disparity between the two quantities. However, when Sheba had numerals substituted for numbers of treats, she immediately began to indicate the smaller

Figure 10.15. Sheba reports the total number of oranges she found distributed among three hiding places (gray circles). After Boysen and Berntsen (1989) with permission.

amount at greater than chance levels. Five more animals tested similarly performed in the same way (Boysen. et al. 1996). When sessions with real objects alternated with sessions using numerals, all the animals performed so as to maximize their rewards when numbers were used but reverted to suboptimal choice with confronted with the actual treats, even after hundreds of trials. Thus even though numerals represent numbers of objects for the animals, the candies themselves arouse an irrepressible “greedy response” that the numerals do not.

The reversed contingency task has subsequently been tried with tamarins, several other monkey species, and all the great apes (see Vlamings, Uher, and Call 2006). Essentially it requires the animal to inhibit its natural response toward the perceptual features of the two piles of food items and be influenced instead by what the relative quantities represent. Substituting numerals for a direct view of the food clearly reduces its perceptual salience, but the same can be done by teaching the animal an association between colors and amounts of food or by simply covering the food containers before the animal chooses. Alternatively, increasing the cost of choosing the larger amount can reduce the number of suboptimal choices (Vlamings, Uher, and Call 2006). Across primates, there may well be species differences in how easy it is to inhibit the tendency to grab a visible larger amount, perhaps related to foraging ecology and sociality, or (on another level) to executive function in the brain, but documenting it will require further work. For example, a comparison of chimpanzees with the other three species of great apes (gorillas, bonobos, and orangutans; Vlamings, Uher, and Call 2006) found that individuals of all species learned the task and did better with hidden than with visible food, but unlike in some other studies the animals were tested with only two combinations of amounts.

10.4.3 Numerical competence without number language

Notice that so far the studies with “number labels” have not actually revealed much about numerical competence per se. This is not true of a recent study of the Munduruku tribe in the Amazon jungle of Brazil (Pica et al. 2004; see also Gordon 2004). The Munduruku have precise counting words for quantities only up to about four. When shown collections of things and asked “How many?” if there are five or more they give varied and vague answers like “some,” “two hands.” Yet when asked to make numerosity discriminations in the comparison and addition tasks depicted in Figure 10.16, they perform almost the same as numerate French controls. Asked to compare clouds of up to 80 dots, their judgments are more accurate as a function of the ratio of the quantities being compared, the same Weber’s Law principle we saw throughout the first part of the chapter. But counting language does make a difference when it comes to precise comparisons. Asked to name or point to the result of an exact subtraction, the tribes people were correct only when the initial amount was four or fewer, whereas the French controls were nearly perfect up to 8 or so, the largest quantities tested. The answer was always within the same small range; what was critical was precise identification of the initial quantity. Along with other studies of children and human adults like those mentioned earlier in this chapter (see also Barth et al. 2006), the study of the Munduruku shows that people share an imprecise representation of numerosity, and perhaps also a precise representation of numerosities up to about 4, with other species, but in addition it shows that one thing language does is to convey precise representation of larger quantities, presumably through counting (see also Dehaene

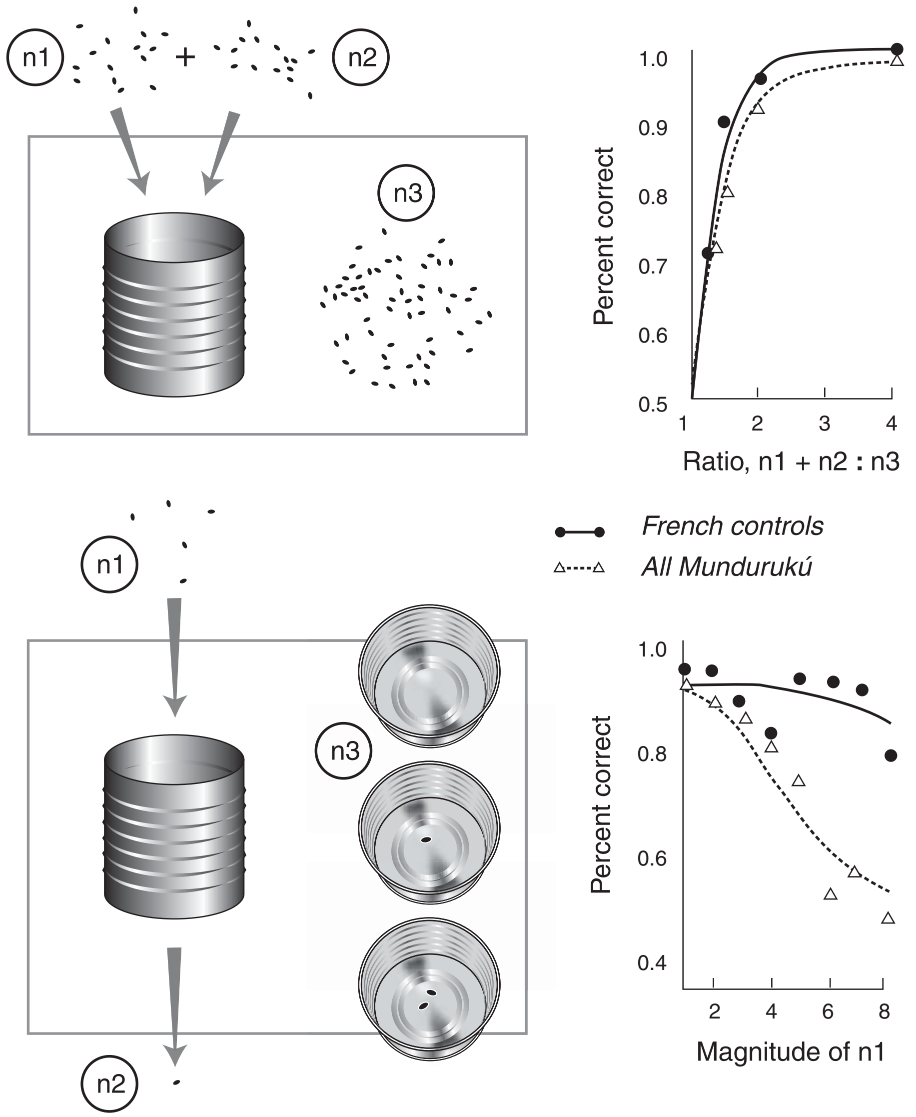


Figure 10.16. Tasks used to test aspects of numerical competence in the Munduruku, with group data compared to that of numerate French adults. In the top task, clouds of n1 and n2 dots successively "fall" into the can and the subject has to judge whether the can holding n1 + n2 items has more or fewer than n3. In the exact subtraction task on the bottom, n1 dots "fall" into the can and n2 "fall out" at the bottom. The subject indicates the number remaining by choosing a can on the right. Adapted from Pica et al. (2004) with permission; samples of the videos presenting these and other tasks to the subjects can be seen in the online supplement to this article.

et al. 2008). Exactly how it does that—for example whether the concept of precise numerosity is built on the small number system—and whether other primitive concepts play a role in mathematical development is a continuing challenge for developmental psychologists (Gelman and Gallistel 2004; Leslie, Gelman, and Gallistel 2008).

10.5 Numerical cognition and comparative psychology

More than any other topic treated in this book so far the comparative study of numerical competence has taken on a whole new look in the last decade. The integrated theoretical and experimental approach that has emerged is exemplary for other areas of comparative cognition. “Can animals count?,” the question that informed most traditional research in the area from Clever Hans onward, is in some ways the least productive kind of comparative question because it impels little more than a search for a yes or no answer. Species either do it or they don’t, and then what? As this chapter illustrates, researchers now are asking something more like, “What are the components of numerical competence, how may they be characterized, what species share which of them, and why (in neurological, functional and/or evolutionary terms)?” A good deal of progress has been made by thinking in terms of two systems, object tracking for quantities up to about three or four, and Weber’s Law based on approximate discrimination among unlimited quantities. However, the exact role and limit, even the existence of, the first of these is still controversial. Discrimination among numerosities seems to imply the ability to order them, but this ability has been studied explicitly mostly with rhesus monkeys. At least in monkeys, the same ability seems to be tapped by learning to order arbitrary items. Whether or not it underlies transitive inference in monkeys remains unclear, as does the relationship of social transitive inference abilities to the performance laboriously elicited in analogous operant tasks. Finally, in the last section of the chapter we see how the numerical abilities of people without language for counting can be understood with the same framework that organizes comparative understanding.

Further reading

Pfungst’s account of Clever Hans has been reprinted in English with an introduction by Robert Rosenthal discussing the general problem of inadvertent cueing and other experimenter influences in psychology (Pfungst 1965). Candland (1993) has written an entertaining and thoughtful book for the general reader that puts Clever Hans–related work with chimpanzees in the context of a long history of attempts to probe the “silent minds” of animals and feral children by teaching them to use language. The chapters by Boysen and Hallberg (2000) and by Emmerton (2001) are good reviews of the history of research on primates and birds, respectively, and the chapter by Terrace (2006) comprehensively reviews serial order learning. Excellent recent reviews encompassing more of the research on specifically numerical cognition highlighted in this chapter are those by Hauser and Spelke (2004) Feigenson, Dehaene, and Spelke (2004), Nieder (2005), and Brannon (2006). Irene Pepperberg’s work with Alex the parrot is comprehensively described in her 1999 book; the studies of parrot numerical cognition are reviewed in Pepperberg (2006).

11

Cognition and the Consequences of Behavior: Foraging, Planning, Instrumental Learning, and Using Tools

A rat that has learned to press a lever for sucrose gets sick in its home cage after drinking sucrose. Next time it is placed in the operant chamber, it does not press the lever.

A chimpanzee emerges from the jungle near a termite mound carrying a slender stick. It slides the stick into a hole in the mound and extracts a mouthful of insects.

The rat and the chimp are exhibiting instrumentally learned behavior, behavior acquired and maintained because of its consequences. We have already encountered instrumental learning, in Chapters 6 (categorization), 9 (timing), and elsewhere, but now we look at the functional and mechanistic principles underlying it. A theme that unites the diverse topics of this chapter is the different senses in which behavior can be described as rational and how they are related (Kacelnik 2006). Just as with Tinbergen's four questions (Chapter 1), these senses are easily confused, with functional issues sometimes mistaken for mechanistic ones and the reverse. In functional terms, we expect behavior to be biologically rational in that it should increase fitness rather than decreasing it: the rat that has learned sucrose makes it sick should no longer press the bar to get it. Rational behavior in economics is similarly defined in terms of function, in this case maximizing utility. Research on instrumental learning and behavior from functional perspectives is the subject of Section 11.1, which introduces optimal foraging models and economic decision-making. Studies of instrumental learning and choice in these contexts have shed light on cognitive mechanisms, and vice versa, but their primary focus is testing functional predictions.

In psychology and philosophy being rational means being able to give a reason for action (Kacelnik 2006). Human folk psychology typically explains the sorts of behavior discussed in Sections 11.2–11.4—acting now for a future benefit, changing a response as its consequences change in value, using tools in given ways—as resulting from explicit causal reasoning. For instance, I shop today because I am planning a party for tomorrow, when the stores will be closed. But behavior may satisfy functional criteria for rationality without resulting from humanlike representations and decision processes. That is, biological rationality may be accomplished by proximate mechanisms that are not psychologically rational. Just as with metacognition (Chapter 7) or spatial mapping (Chapter 8), much research on the topics in this chapter reflects a fundamental tension between anthropomorphic, folk-psychological explanations and "simpler" ones, usually based on associative learning. Here the challenge is to translate intuitive predictions based on how people reason (or believe they reason) about causes and effects into unambiguous nonverbal tests. How can we tell, for instance, what a chimpanzee getting termites with a stick understands about how the tool works?

11.1 Foraging

A starling walking across a pasture pokes its beak into the ground and pulls out a leatherjacket (*Tipula* larva). When it has three larvae lined up in its beak, it flies off, carrying the load of prey to its nestlings (Figure 11.1). Watching starlings foraging for larvae, a behavioral ecologist would ask "What *should* these animals do, and do they do it?" However, as the study of foraging in behavioral ecology evolved, it incorporated and in turn contributed to answering the psychologist's question, "*How* do these animals do whatever they do?" Indeed, the study of foraging is one of the best examples of how functional and mechanistic approaches to behavior can be integrated (Real 1991; Dukas 1998 ; Stephens, Brown, and Ydenberg 2007; Shapiro, Siller, and Kacelnik 2008). This section begins with a brief overview of foraging theory. Then we look at a sample of classic foraging problems illustrating interactions between tests of optimality models and studies of information-processing and decision making (for a more through review see chapter 9 in Shettleworth 1998). Finally we look at recent work flowing from the analogy between foraging and consumer choice (Section 11.1.5).

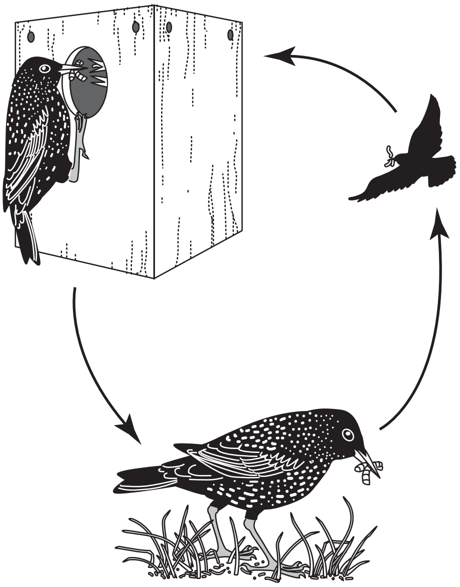


Figure 11.1. Foraging by starlings and other birds while feeding young consists of cycles of traveling to suitable patches of the environment, collecting prey, and flying back to the nest.

11.1.1 Foraging theory

Optimality models in behavioral ecology start with the assumption that behavior has been selected that maximizes fitness (Stephens and Krebs 1986; Parker and Maynard Smith 1990). Because fitness (Box 1.2) is often difficult to measure directly, foraging models usually deal in a more easily measured *currency* that is assumed to contribute to fitness. Very often this is net rate of energy intake, that is, energy consumed minus the energy expended to obtain it, a currency that does demonstrably influence fitness (e.g., Lemon 1991). The formal characterization of a foraging situation also includes *constraints* on the forager. For example, consider a visual forager like a lapwing walking across a meadow scanning the ground for insects (Figure 11.2). How far should the bird move between scans? Walking consumes energy, so the cost of moving increases linearly with the number of steps the bird takes. However, the chance of spotting a new prey item increases as the bird moves away from the area it has just scanned. If the bird can scan a circular area, it should move just the diameter of one scan before stopping to scan again (O'Brien, Browman, and Evans 1990; Parker and Maynard Smith 1990). As illustrated in Figure 11.2, the tradeoff between the cost of moving and the benefit of scanning a new patch can be quantified to compute the course of action that maximizes the lapwing's net rate of energy intake. In this example, the bird's visual system imposes psychological constraints, and the structure of the world in the form of the bird's physiology and the distribution of prey imposes physical constraints.

11.1.2 When to leave depleting patches: The marginal value theorem

In the first of the classic foraging models we consider, prey are in distinct *patches* separated by areas without prey, and the predator depletes patches as it feeds. (All food items are *prey* in this context even if they are grass or seeds.) As items become sparser the forager will experience diminishing returns, so it must decide when to leave the current patch and travel to the next one. The situation confronting starlings collecting leatherjackets to feed their young (Figure 11.1) is formally identical because it takes longer to collect each larva the more it already has in its beak. Thus even if the patch does not deplete appreciably, the rate of gain decreases the longer the starling searches for prey between trips back to the nest.

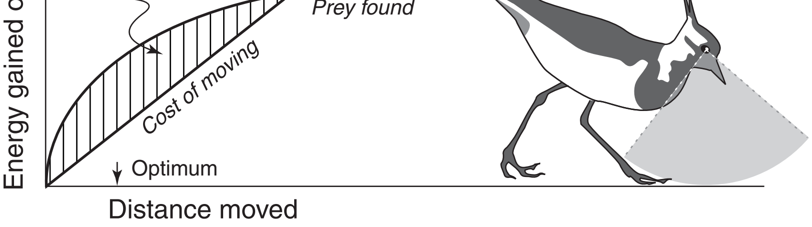


Figure 11.2. Graphical calculation of the optimal size of move for a foraging lapwing. The optimum is the point where the distance between energy intake and energetic cost of moving (the net energy intake) is maximal. After Parker and Maynard Smith (1990) with permission.

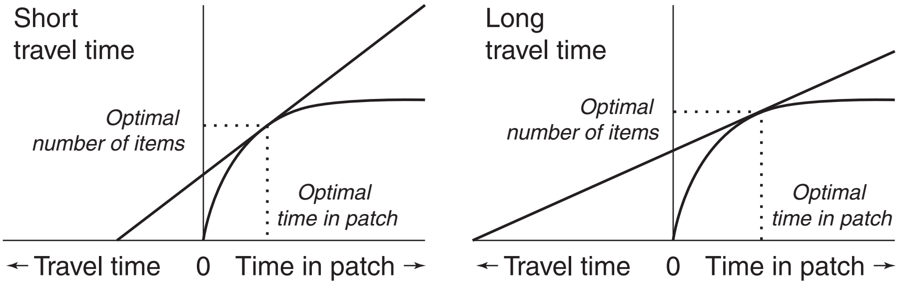


Figure 11.3. Graphical calculation of optimal patch residence time according to the marginal value theorem. Energy gain is in the vertical dimension. The slope of the diagonal line in each panel is the maximum net rate of energy intake in an environment with the given travel time and gain function (items vs. time in patch). The slope will necessarily be less if the animal stays a longer or shorter time.

Intuitively, a forager should stay longer in one patch if the next patch is likely to be far away than if it is close by. For the starling collecting leatherjackets, it makes sense to gather a large load when far from the nest, but to start home with a small load when close to the nest. The solution to the problem of maximizing energy gain in depleting patches, shown in Figure 11.3 is known as the *Marginal Value Theorem,* abbreviated *MVT* (Charnov 1976). To a first approximation, this is a good account of what animals do (Stephens and Krebs 1986; Nonacs 2001). To maximize its overall rate of energy intake, a forager should leave a patch when the rate of energy gain in that patch falls to the average rate in the habitat. Before this time, the forager is by definition doing better than it can do elsewhere. Afterward, it could do better on average by leaving. In order to behave in this way, a forager has to keep track of its current rate of intake. If prey come in discrete similar-sized units like leatherjackets in a field, this means accumulating information about times between prey captures. The forager also needs information about the average intake rate in the rest of the habitat.

The foregoing analysis suggests that foraging close to optimally might mean storing information about travel times and intercapture intervals, in which case the data about timing in Chapter 9 might help to explain what animals do. However, sometimes simpler mechanisms can do the same job. For instance, a flowering plant with multiple blossoms on a single stalk is a patch for a foraging bumblebee. The bee can search it efficiently by using a simple *rule of thumb,* “start at the bottom, move up, and leave when you reach the top” (Pyke 1979), that is, it can respond to a simple reliable cue in a fixed way. *Nemeritis canescens* (now known as *Venturia canescens*) is a parasitoid wasp that lays eggs in the larvae of flour moths. The female wasp searching for hosts in a granary walks about on the substrate. When she encounters a patch of chemicals secreted by the host, she stays in it by turning back whenever she comes to the edge of the patch. The wasp’s behavior can be modeled as a process in which responsiveness to the host chemical (reflected in the tendency to turn back into the patch upon reaching the edge) habituates with time in the patch but increases with each oviposition (Waage 1979). A single oviposition has maximum effect; the effect of the next one depends on how much later it occurs, as shown in Figure 11.4. This simple mechanism keeps the wasp longer in a good patch because abundant prey frequently push responsiveness back up, but it allows her to leave after long

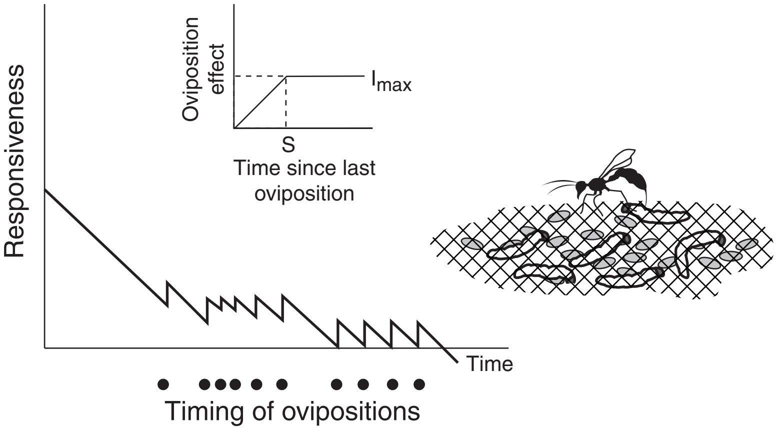


Figure 11.4. Model of patch residence time in *Nemeritis*. The inset shows the increase in responsiveness as a function of time since the last oviposition. When responsiveness to the current patch falls to zero, the wasp leaves. Redrawn from Waage (1979) with permission.

enough without encountering prey. However, other populations of these wasps which lay their eggs in fallen fruits seem to use a different rule (Driessen et al. 1995), a finding which raises the interesting question of whether and how these wasps change their ways of responding in different environments.

The simple combination of sensitization and habituation that governs the wasp's behavior can be contrasted with decision making based on memories for interprey intervals and travel times. Because memory for times is not perfectly accurate but follows Weber's Law (Chapter 9), timing acts as a psychological constraint preventing animals from behaving precisely optimally. The best examples of how it does so come from a program of research on starlings by Kacelnik and his colleagues that combined experiments in the field and in an operant simulation of patch choice in the laboratory (Kacelnik and Cuthill 1987). Here, the "patch" was a pecking key in the middle of one wall of a long cage, and the birds "traveled" from one patch to another by flying between two perches a number of times (Figure 11.5). Completing the travel requirement reset the patch to the shortest interprey interval, as if the bird had arrived in a new patch. If the "patch" delivers a varying number of prey (crumbs from a feeder) at equal intervals and then depletes entirely, the bird should depart as soon as the current interval exceeds the remembered standard interprey interval. But because timing obeys Weber's law, the time of leaving the patch has a variance proportional to the interprey interval (Brunner, Kacelnik, and Gibbon 1992, 1996).

Pecking rate peaked at the value of the interprey interval, with a broader distribution of response rate versus time at longer intervals just as in experiments with the peak procedure (Section 9.2). In addition, the birds waited longer after the expected time for an item before leaving a patch with a long interprey interval, as if their decision took into account the greater error in their ability to detect depletion of a less dense patch (Figure 11.6). The situation in this experiment was not exactly the same as the one addressed by the marginal value theorem because the experimental patch offered prey at fixed intervals and depleted abruptly, but it mimics the situation experienced by animals that prey on swarms of insects. For example, spotted flycatchers (*Muscicapa striata*) stay at a perch while a swarm of insects is within range, sallying out to capture prey at roughly constant intervals. They leave for another

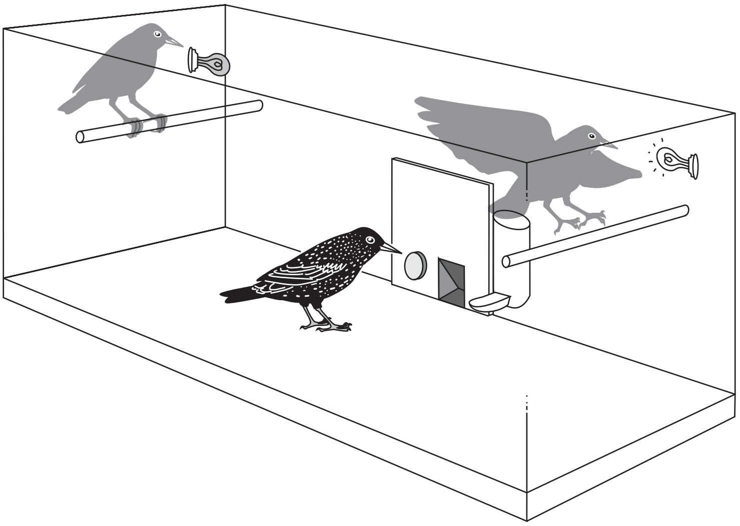


Figure 11.5. Setup used to study patch choice in captive starlings. To travel between patches, the starling hops from the perch with the light off to the one with the light on; the light at that perch then goes out and the opposite light goes on, and so on until the travel requirement is completed. Water is available from the device beside the feeder and pecking key. Redrawn from Brunner, Kacelnik, and Gibbon (1992) with permission.

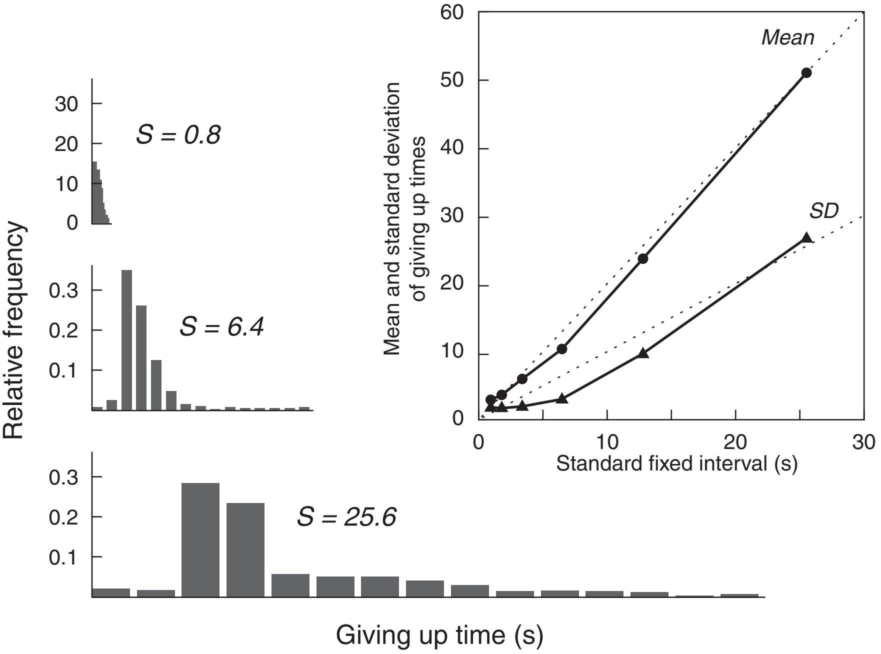


Figure 11.6. Relative frequency of giving up times of different lengths (in seconds) at three of six standard interprey intervals tested. The inset shows the means and standard deviations of the distributions at all six values. Dotted lines are regressions fit to the data. Redrawn from Gibbon and Church (1990) with permission.

perch after a time without prey that is approximately 1.5 times the regular interprey interval (Davies 1977; see Kacelnik, Brunner, and Gibbon 1990).

11.1.3 When to attack

In the classic model of prey choice within patches the forager encounters items successively, and it can accept each one as encountered or reject it and go on searching (Figure 11.7). Acceptance entails devoting a *handling time* to the item, time which cannot be devoted to searching. Pulling the sting off a bee, shelling a nut, extracting nectar from a flower, tearing apart a carcass: all require handling time. In the simplest case the predator recognizes prey types immediately and ranks them in terms of the energy they yield per unit of handling time (E/H). Energy per unit of time foraging can be maximized by accepting all prey items when prey density is low but accepting only the better items (i.e., those with the highest E/H) when prey density is high. If there are just two item types, the predator's behavior toward the poorer items should reflect the density of better items: reject poor items when good items are abundant, otherwise accept them. There is a threshold of good item abundance at which the forager should switch from rejecting to accepting poor items. This policy makes good intuitive sense: when the world is a good place as regards food, mates, homes, a creature can afford to be choosy, but when times are tough, it should take whatever comes along.

The simple optimal prey selection model has qualitative but not always precise quantitative support from redshank selecting worms in mudflats (Goss-Custard 1977), great tits picking mealworms off a conveyor belt in the laboratory (Krebs,. et al. 1977), pigeons pecking key colors paired with different delays to reinforcement (Fantino and Abarca 1985; Shettleworth 1988), and many other tests (Sih and Christensen 2001). An almost universal deviation from optimality is that acceptance

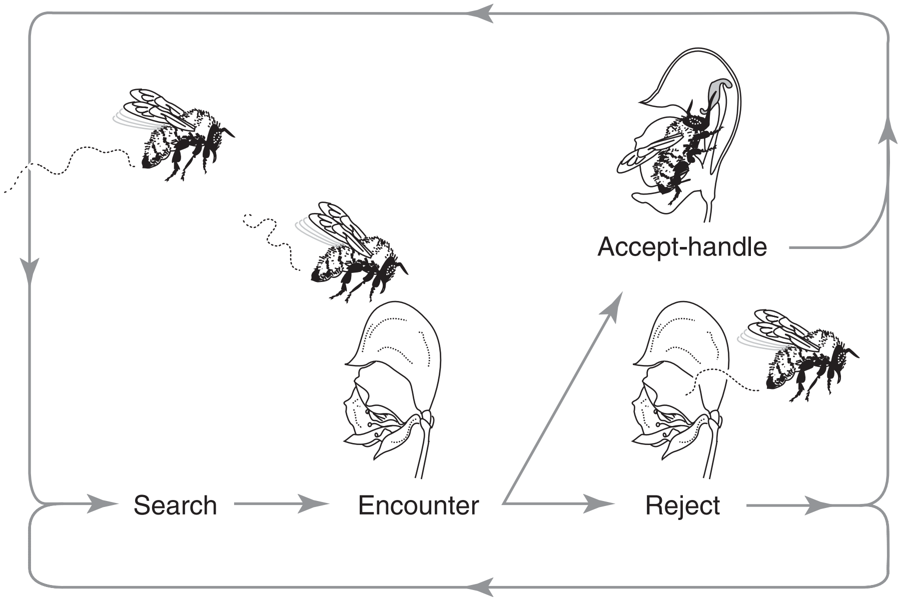


Figure 11.7. The cycle of events in prey choice.

of relatively poor items is seldom all or nothing: at an intermediate abundance of better items some poor ones will be taken and others rejected. Given that perception and memory generally have some degree of error, this is not surprising.

Just as in patch departure, animals may use rules of thumb, relying on simple cues that generally predict prey quality like size (Barnard and Brown 1981). But learning about prey profitability, for example one's own competence at handling a kind of prey, can lead to individual and developmental differences in prey preferences (e.g., Sullivan 1988). A similar variety of mechanisms contributes to assessing prey abundance. For example, prey catching is a reflex in the mantid *Hierodula crassa* (Charnov 1976), but the animal's tendency to strike at flies is modulated by the fullness of its gut. Only nearby flies are attacked when the gut is full; more distant prey become attractive as the gut empties. The apple maggot fly's acceptance of fruit in which to lay her eggs can be modeled like the wasp's oviposition (Figure 11.4), as reflecting a threshold which changes with recent ovipositions and host encounters (Mangel and Roitberg 1989). In contrast, animals trained on operant analogues of prey learn both the delays to food associated with each of two or more signals ("items") and the intervals between them. Animals trained on such schedules do accept nearly all the better "items" offered, and the effects of changing the frequency or profitability of items are seen in the choice of poor items. At the moment of encounter with an item, the animal is choosing between the handling time (or delay to food) associated with that item and a second, variable, delay to food composed of the average time to another item plus the expected time to handle that item. Accordingly, behavior on such schedules, studied mostly with pigeons, is consistent with the mechanistic models of timing and choice discussed in the next section (Shettleworth 1988).

Models of optimal prey selection make one prediction not anticipated by information about behavior on conventional reinforcement schedules: as the time available for foraging, the *time horizon,* grows short, animals should become less choosy, accepting more poor items even when better items are abundant (Lucas 1983). It is easy to see why. If the time available for foraging is about to run out, there may not be enough time to encounter any more items, so the best bet is to take the item at hand. Observations with natural prey items conform to this prediction. For instance, in 3-minute and 6-minute foraging bouts, shrews accepted both large and small mealworm pieces, whereas they rejected small pieces in 9-minute bouts (Barnard and Hurst 1987). In an operant analogue of prey choice, pigeons that had 10-minute sessions in one distinctively decorated operant chamber and 20-minute sessions in another accepted fewer poor items in the first 10 minutes of 20-minute sessions (i.e., when the time horizon was relatively long) than in a 10-minute session (Plowright and Shettleworth 1991). These observations provide reason to question the tradition of treating length of conditioning sessions as a variable of no interest, to be determined mainly by convenience.

11.1.4 Choosing among patches: Matching, sampling, and risk

When patches don't change, foragers face a situation much like that in traditional studies of *concurrent schedules of reinforcement.* As the name implies, on such a schedule two or more reinforcement schedules run concurrently, each associated with a different lever, pecking key, or the like, and at any moment the animal can choose which one to respond to. Historically students of behavior on concurrent schedules have been most interested in the *steady state,* that is, behavior after many sessions of exposure to the same conditions. When both schedules are *fixed* or *variable ratios* (i.e., reinforcement for exactly or on average every *n*th response) the steady state is the relatively uninteresting one of nearly exclusive choice of the more favorable response: reinforcer ratio. Much more influential have been studies of behavior with concurrent *fixed* or *variable interval* (*FI* or *VI*) schedules. On a VI schedule interreinforcement intervals are randomly distributed with a mean specified by the VI value. Thus on VI 20 seconds, reinforcement is available on average every 20 seconds, but with interreinforcement intervals that may range from effectively zero to much longer than 20 seconds. Once it becomes available, a reinforcer typically remains available until the animal responds, as in a repleting patch in which there are no competitors. Such a situation is experienced by wagtails foraging for dead insects washing up along riverbanks (Houston 1986) or traplining territorial hummingbirds (Chapter 9).

Reinforcers can be maximized on a concurrent VI VI (*conc VIVI*) schedule by continually switching back and forth, checking each alternative in turn to see whether a reinforcer has become available there (Houston and McNamara 1981). This is what animals do, even when direct reinforcement for switching has been reduced by imposing a *changeover delay* so reinforcers cannot be collected until a few seconds after switching. But more than just working on both options, animals match the proportion of time spent or number of responses made at an alternative to the proportion of reinforcers obtained there (Herrnstein 1961). This relationship, illustrated in Figure 11.8, has been found so consistently in so many species and situations that it is referred to as *the Matching Law* (review in Williams 1988; Staddon and Cerutti 2003). Animals match behavior not only to numbers of reinforcers but also to reinforcer amounts or delays, in general to any correlate of reinforcer value. Indeed, because matching can be assumed to obtain very generally, preference on conc VI VI schedules is used to assess the relative values animals place on different commodities (e.g., Hamm and Shettleworth 1987; Deaner, Khera, and Platt 2005).

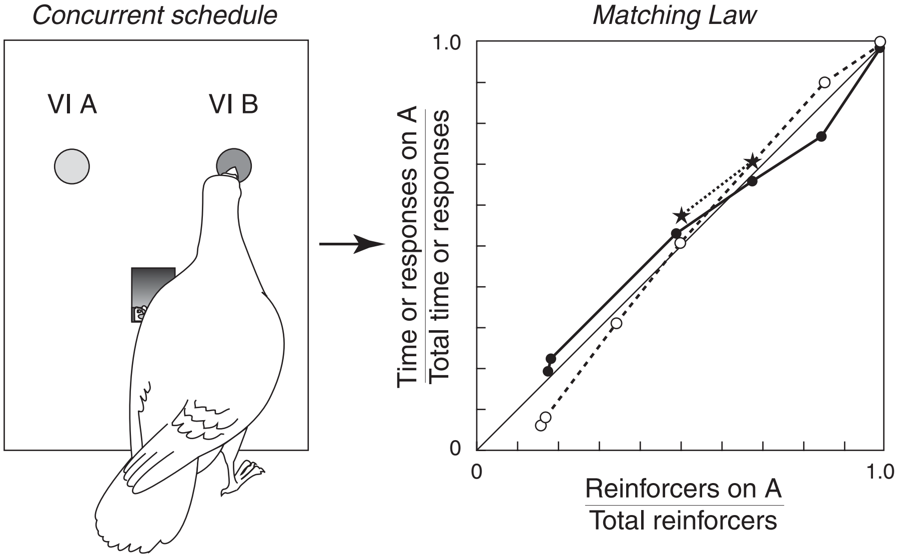


Figure 11.8. Typical experimental setup for studying behavior on concurrent schedules of reinforcement and data illustrating the matching law. Solid diagonal line is perfect matching. Each symbol represents data from a different pigeon. Data redrawn from Herrnstein (1961) with permission.

How do animals match?

Much research has been devoted to understanding what mechanism is responsible for matching, but there is still no completely satisfactory answer (Williams 1994; Staddon and Cerutti 2003). For example, if animals match because matching actually maximizes reinforcers, responses should be allocated in some other way if maximizing requires it. However, when pigeons are required to respond on a seldom-reinforced alternative to advance the schedule on a more frequently reinforced one, they still match relative responding to relative reinforcers obtained even though by doing so they earn fewer reinforcers than they could (Mazur 1981; Williams 1988). The mechanism that brings about matching on concurrent VI VI schedules may have evolved because it results in maximizing fitness under natural conditions, but it does not seem to consist of comparing total intake after allocating choices in different ways and adopting the policy that gave the most food (Houston 1987).

A more successful approach is the SET (Scalar Expectancy Theory) model of choice (Gibbon et al. 1988). Each delay to food experienced is assumed to be remembered in the fuzzy way described by Weber's Law. Faced with a choice between two or more alternatives, an animal is assumed to sample from the distribution of remembered delays associated with each alternative and choose the alternative with the shortest sample on that trial (Figure 11.9). In effect this is a model of maximizing

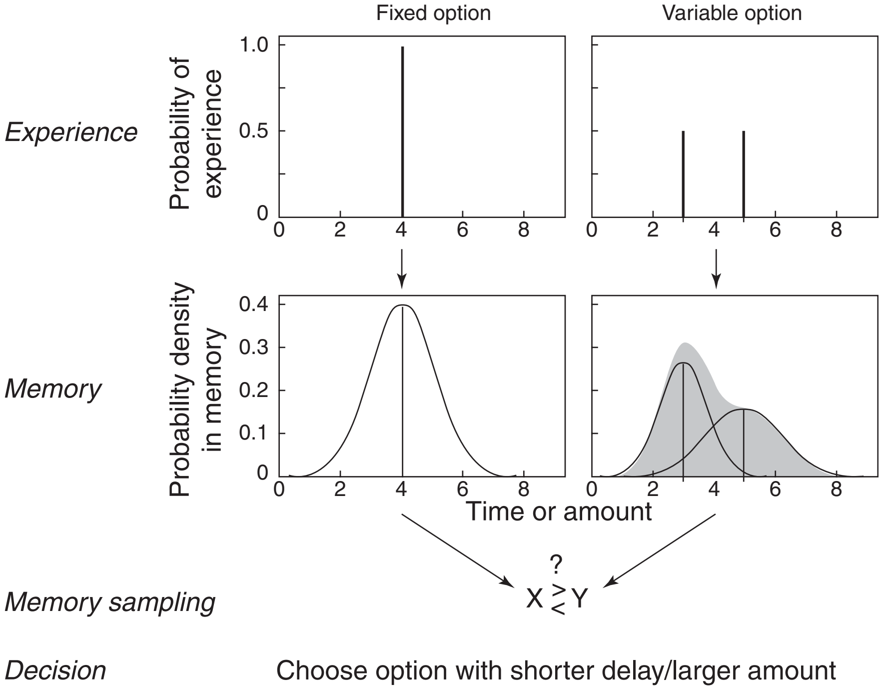


Figure 11.9. The scalar expectancy account of choice between a fixed schedule of reinforcement and a variable schedule with the same mean amount or delay. For simplicity, in this example the variable schedule has two equiprobable values. Reinforcer value decreases with delay but increases with amount. Thus if the units on the x-axis correspond to actual delays and amounts, short delays or small amounts will be overrepresented in the summed probability distribution (gray). After Bateson and Kacelnik (1995) with permission.

rate under a psychological constraint. It does predict matching on concurrent VI VI schedules (Gibbon. et al. 1988). It also explains why animals prefer a variable delay to food (VI schedule) to an FI schedule with the same mean, a finding that cannot be explained as maximizing. As shown in Figure 11.9 for the simplest kind of case, because the memory distribution for a VI has an overrepresentation of short intervals, a sample taken at random is more likely to represent a relatively short interval than is a random sample from the equivalent FI schedule. As this account predicts, pigeons do not prefer a VI schedule constructed so that its memory distribution more closely resembles that from a fixed schedule giving the same mean number of reinforcers per session (Gibbon et al. 1988). The same approach explains why the reverse is true with amounts: a fixed amount is preferred to a variable amount with the same mean (Figure 11.9).

On a roughly equivalent alternative account shortly discussed in more detail, the value of a reward declines disproportionately (hyperbolically or proportionally with 1/time, Mazur 2001) as it is delayed from the moment of choice. Such *discounting* means that the average value of reward in the VI is greater than in the FI. Consistent with the data on temporal bisection in Chapter 9, both accounts predict that a mixture of two equiprobable intervals like that in Figure 11.9 should be psychologically equivalent to a fixed interval with their geometric mean. Mazur (1984) examined such equivalences by training pigeons in a *titration procedure*. Trials occurred in cycles consisting of forced exposure to the current values of a fixed and a variable option followed by opportunities to choose between them. If birds preferred the FI in those trials, it would be made slightly longer in the next cycle whereas if they preferred the VI, the FI would be shortened. This procedure eventually homes in on an FI value psychologically equivalent to the given VI. For example, consistent with scalar timing or hyperbolic discounting, the birds were indifferent between a mixture of 2-second and 18-second delays and a fixed 6-second delay.

The discussion so far assumes that choice between schedules is based on an accumulation of experience, implying that matching develops slowly. However, under some conditions animals respond extremely quickly to changes in times between rewards. Experimentally naive mice show matching as soon as they learn to use two food hoppers that deliver pellets at different rates (Gallistel et al. 2007). And rats exposed to concurrent VI VI schedules of positively reinforcing brain stimulation that change once per session switch their preference within as little as one interreward interval (Mark and Gallistel 1994). They also track random fluctuations in the times between rewards on each schedule. Functionally, frequent changes in the environment should favor immediate tracking, or a short *memory window,* whereas stability should favor storing long-term experience (Cowie 1977), but it is unclear whether this informal functional prediction provides an account of these findings.

Sampling and choice

How much experience should be used to estimate the quality of reward schedules is one example of the more general functional problem of information use in foraging. This is not necessarily one single problem but a set of problems requiring different models (Stephens 2007). An example that brings together an optimality model with the SET model of choice is depicted in Figure 11.10. Here, the animal chooses between a constant mediocre patch and a fluctuating patch where prey occasionally become very abundant. At other times, prey are scarce in the fluctuating patch, and

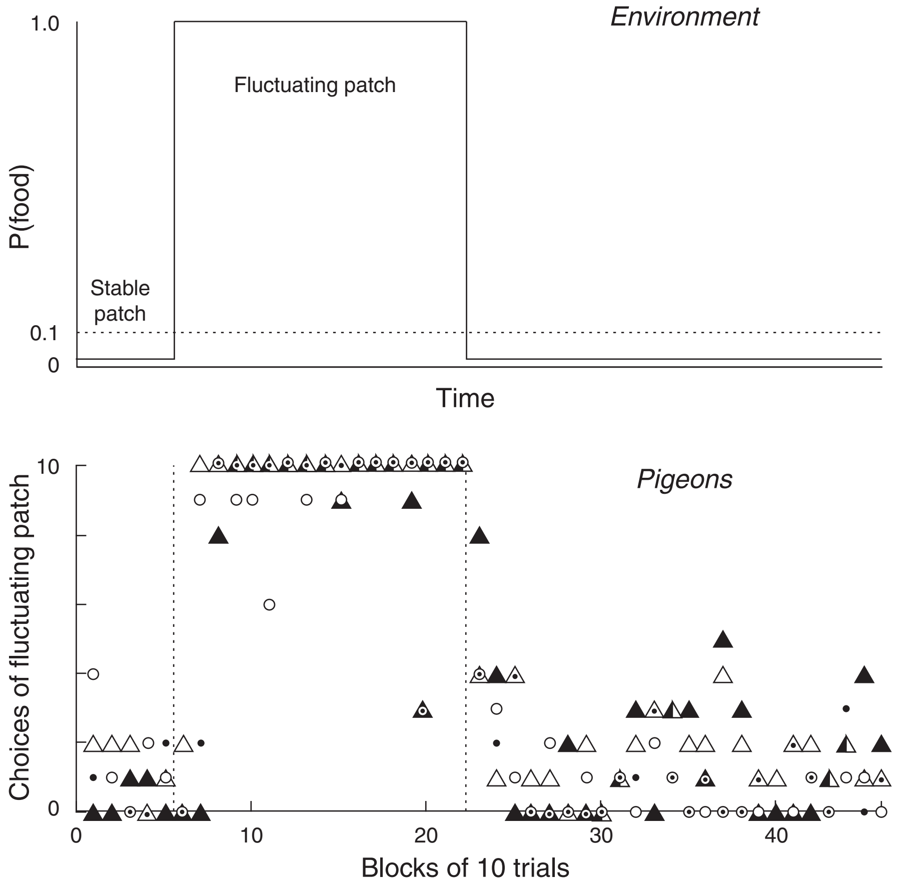


Figure 11.10. Contingencies ("Environment") and data ("Pigeons") from the experiment on environmental tracking described in the text. The four symbols in the lower part of the figure represent data from four different birds. Choices of the fluctuating patch while p(food) = 0 there are sampling responses. Redrawn from Shettleworth et al. (1988) with permission.

the forager is better off in the mediocre patch. If there are no cues to the state of the fluctuating patch, intake is maximized by occasionally visiting the fluctuating patch to sample its state. If it is better than the constant patch, the animal can stay there until prey become sparse again. The optimal behavior in this situation (Stephens 1987) is to sample at fixed intervals—for instance, every tenth foraging trip—rather than at random. This makes sense because sampling too soon will not allow enough time for the patch to change state whereas waiting too long could result in missing some of the good state. Sampling should increase when the constant patch becomes worse or the fluctuating patch's good state becomes better: in both cases there is more to be gained by sampling.

In a test of these predictions (Shettleworth et al. 1988; see also Stephens 2007), pigeons were trained in a long operant chamber with a "patch" at each end. The "fluctuating patch" switched fairly frequently between a schedule delivering no food (extinction) and one delivering food at a high rate. Although the birds sampled occasionally as predicted and switched to the fluctuating patch when it was good (Figure 11.10), behavior deviated from the predictions of the optimal sampling model in three ways. *(1)* Sampling occurred at random, not at regular intervals. *(2)* Sampling frequency did not change when the reinforcement probability in the good state varied. *(3)* When the fluctuating patch was good, the birds occasionally visited the constant patch, a sort of "reverse sampling" that reduced their reward rate. The SET model nicely accounts for all these findings. For instance, visits to the fluctuating patch are random because random samples are taken from memory, and sampling behavior occurs when the shorter memory sample comes from the fluctuating patch. Thus although this situation can be described as one in which animals are collecting information by sampling, here "sampling" is not some special category of behavior reinforced by the information it brings. Rather, the pigeons learned the reinforcement schedules associated with each option and chose accordingly. Box 11.1 discusses other situations in which sampling is optimal.

Box 11.1 Foraging for Mates and Homes

Although optimal foraging and its relationship to psychological studies of food-rewarded behavior are emphasized in the main text, optimality modeling has also been applied to searching for and choosing other resources such as mates and nests. Sexual selection theory predicts that, especially in species in which each offspring demands substantial investment by its mother, females should search for and choose the best males to mate with. But choosiness has a cost in that if the female spends too long searching for a mate, the breeding season may pass or the chances of raising offspring successfully before winter may decline. On one model of optimal mate choice (review in R. Gibson and Langen 1996; Sherman, Reeve, and Pfennig 1997), *best of n,* the female inspects *n* males and then mates with the best. The optimal number is determined by the time and energy costs of searching (Janetos 1980). This seems to require that females remember all the sequentially inspected males equally well, that is, without forgetting or primacy or recency effects. An alternative model with less unrealistic assumptions about memory is that the female mates with the first male she encounters who surpasses some threshold value. The threshold should be determined by the average quality of males in the environment: a male of poor quality in absolute terms may be acceptable if most males are even poorer. Both of these models imply that quality is recognized perfectly and immediately. But as we know from Chapter 3, imperfect recognition is more likely, in which case repeated visits to each male might improve a female's estimate of his quality. This assumption is embodied in a third model of optimal mate choice, the Bayesian assessment model (Luttbeg 2002).

Because which model predicts the highest fitness depends on such factors as how much time is available and the cost of assessment (Luttbeg 2002), species differences in mate choice might be expected. Females of many species do have encounters with more than one male before mating, and as predicted by the best of n and the comparative Bayesian models, males who have been inspected and rejected are sometimes reinspected and accepted (Gibson and Langen 1996; Weigmann et al. 1996). The threshold model also permits choosing a previously rejected male if the threshold is continuously adjusted on the basis of experience. Consistent with this, data from birds (e.g., Collins 1995) and fish (e.g., Bakker and Milinski 1991) reveal a contrast effect: a mate of a given quality is more likely to be preferred the lower the quality of previously encountered males. Another factor that may complicate the picture is that rather than sampling males for herself, a female may copy the mate choice of earlier-arriving females (Chapter 13 and Sherman, Reeve, and Pfennig 1997).

For species that disperse from their natal territory, choosing a place to settle presents the same functional and mechanistic problems as mate choice in that a single decision has large implications for fitness (Mabry and Stamps 2008). In one attempt to infer the decision rules being used, Mabry and Stamps (2008) radio-tracked dispersing brush mice over several days as they visited areas around their natal nest before settling in a nest of their own. The mice most commonly behaved as if using a comparative assessment mechanism, visiting each of a relatively small number of areas several times before settling in one. Since a potential territory likely has multiple relevant features, such as the presence of food, shelter, and competitors, it is perhaps to be expected that animals would need time to assess them. What and how animals learn about habitat quality offers many possibilities for future investigation (Mabry and Stamps 2008). Because more than one feature of a potential mate or territory may be relevant for optimal choice, the economic model discussed in Section 11.1.5 also applies to choice of mates and territories, although as yet little is known about whether these choices are also context-dependent (Bateson and Healy 2005; Royle, Lindstrom, and Metcalfe 2008).

Risk

Preference for a VI schedule over an FI that delivers food at the same mean rate, discussed earlier in this section, is a puzzle if one assumes that foragers are maximizing net rate of energy intake. But variance should matter under some conditions. For example, as a small bird nears the end of a winter day, what it can find in an unvarying patch may not be enough to get it through the night. Its only chance for survival might be in a risky (i.e., variable) patch that occasionally yields a bonanza. This argument leads to the *energy budget rule:* an animal below its energy budget should choose a risky option over a certain option with the same mean, that is, it should be *risk prone*. Otherwise, the forager should be *risk averse* (Stephens 1981; McNamara and Houston 1992). Risk sensitivity is expected in the context of any interruption like the end of the breeding season, the beginning of migration, or the arrival of predators (McNamara and Houston 1992).

Risk sensitivity has been sought in species that include bees, shrews, pigeons, starlings, and juncos (Kacelnik and Bateson 1996; Brito e Abreu and Kacelnik 1999) as well as in people (Weber, Shafir, and Blais 2004). As in Mazur's (1984) experiment already described, in such studies animals typically have "forced" trials with a fixed and a variable option (e.g., 4 items of food on the left and a 50:50 mix of 1 item and 7 items on the right). Subsequent free choices between the options reveal whether the animal is *risk prone* (i.e., prefers the variable option), *risk averse,* or indifferent to risk. As we have seen, animals generally prefer variable over fixed delays to food (i.e., they are risk prone in delay) but with variance in amount they are generally risk averse or indifferent (reviews in Kacelnik and Bateson 1996; Bateson and Kacelnik 1998; Kacelnik and Brito e Abreu 1998). Figure 11.9 shows how the SET approach explains these outcomes.

Risk sensitivity implies that animals do not represent rates of intake only as long term averages (i.e., $\Sigma E/\Sigma T$). A possibility consistent with SET is that instead they store and average short term rates, that is, the average of item-by-item E/T. This makes less demand on memory than long-term averaging because an animal has direct information about the most recent interprey interval and prey size each time it collects a food item. Memory for short intervals may also be favored because it is more accurate than memory for longer ones (see Chapter 9 and Stephens, Kerr, and Fernández-Juricic 2004). In a careful series of experiments using variance in both amount and delay, starlings' choices were consistent with maximizing short-term rates with only the times during the trials taken into account, that is, without the intertrial intervals (Bateson and Kacelnik 1995; 1996, 1997). Expected times to the next feeding(s) seem to determine "risky" choice, not unpredictability of the outcome in itself. Given a choice between two sequences of interreward intervals with equal variance but different degrees of predictability, starlings preferred the predictable string mainly when it began with a comparatively short delay to food, as if discounting later rewards in the sequence (Bateson and Kacelnik 1997). Such steep discounting of future rewards seems inconsistent with the suggestion that animals plan ahead discussed in Section 11.2.

The energy budget rule seems to imply that the way in which outcomes are valued or compared changes with how close the animal is to meeting its energetic requirements, a factor not usually taken into account in psychological theories of choice. In fact, however, experimental tests of the energy budget rule have not given much evidence to support it (Kacelnik and Bateson 1996; Brito e Abreu and Kacelnik 1999). Regardless of energy budget, animals prefer variable delays to food over a fixed delay equal to their mean, but effects of energy budget have sometimes been found in experiments with variance in amounts of food (e.g., Ito, Takatsuru, and Saeki 2000). Effects of energy budget seem to be found more often with small than with big animals, which makes functional sense because a small animal is less likely to have the reserves to survive a temporary shortfall than is a large one. However, such an effect of body mass remains to be documented in a proper comparative test (Brito e Abreu and Kacelnik 1999). In any case, it is difficult to change correlates of energy budget such as the rate of food intake during an experiment without changing experimental parameters that might by themselves influence choice. For example, in the original test of the energy budget rule (Caraco, Martindale, and Whittam 1980), juncos on a negative energy budget were tested later in the day and with longer intertrial intervals than birds supposedly on a positive energy budget, and to equalize overall rates of intake larger amounts of food were followed with longer delays until the next trial, thereby confounding variability in amount with variability in delay. To some extent such problems were overcome by testing birds at two temperatures in a later study (Caraco et al. 1990). The birds tended to be risk averse at the higher temperature and risk prone at the lower one. In the next section and in Section 11.3 we see that the subjective value of food can depend on the circumstances in which it has been experienced. Such *incentive learning* might also lead to apparent energy budget effects in some circumstances.

11.1.5 Foraging and economic decision-making

At first glance there is a compelling parallel between optimal foraging theory and economic theory. Foraging theorists depict animals as maximizing fitness; economists depict individuals as maximizing *utility*. But utility is not fitness; it is a presumed currency of subjective value that economic decision makers are assumed to be maximizing in a consistent way. Still, because evolution would almost by definition be expected to select for creatures that value whatever increases their fitness, under natural conditions maximizing subjective utility and maximizing fitness ought to come to the same thing. This suggests that looking at animal behavior in situations comparable to those studied by economists should produce parallel outcomes and perhaps new insights into the evolution or mechanisms of economic behavior. Indeed, research on the neural mechanisms of economic decision making is thriving in the new field of neuroeconomics (Glimcher and Rustichini 2004; Sanfey et al. 2006). Such research analyzes how probability and value are represented in primate brains, using imaging with humans and single cell recordings with monkeys performing instrumental choice tasks.

Some important contemporary research in economics deals with psychological mechanisms for evaluating and deciding among options. Surprisingly often people rely on rules of thumb, referred to in this context as *heuristics,* simple decision rules that work pretty well in natural conditions but violate utility maximizing in contrived ones (Todd and Gigerenzer 2007). Thus, as in the study of foraging, behavior that meets a functional criterion of rationality occurs in the absence of psychological rationality. Further evidence that economic choices do not necessarily involve literal representation of the variables being maximized comes from the irrational choices reliably shown in certain circumstances. As discussed next, attempts to capture such apparently irrational economic choices with animals in a foraging context has led to a productive analysis of the underlying psychological mechanisms (for other examples see Chen, Lakshminarayanan, and Santos 2006; Padoa-Schioppa, Jandolo, and Visalberghi 2006).

Comparative evaluation

A key assumption of economics is that people maximize utility *in a consistent way.* Among other things, this means that choices are transitive and *independent from irrelevant alternatives.* The latter means that A is preferred to B whether or not other options are present. This principle may be violated when the options differ on two dimensions as illustrated in Figure 11.11. Here we are concerned with preferences between a target item, T, and a competitor, C, that is more attractive than T on one dimension and less on another, such as costing less but being smaller. In many examples with real products, introducing a third option, the *decoy* (D), that is the same as the target on one dimension and lower-valued (i.e., less preferred) on the

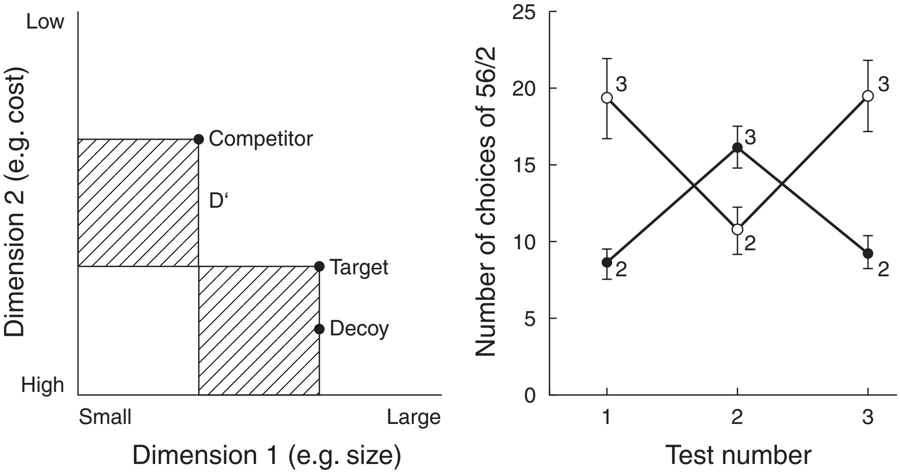


Figure 11.11. Left: the target, competitor, and decoys described in the text in the two-dimensional space of cost versus size. Note that the cost axis represents cost from high to low; thus items higher in this dimension are lower-priced and therefore valued more. The asymmetrically dominated decoy effect will occur for decoys D or D' respectively within the adjacent shaded areas. Adapted from Bateson, Healy, and Hurly (2003). Right: mean number of times gray jays chose the target, 2 raisins 56 centimeters down a tube, in a binary choice (2) and a trinary choice (3) with the decoy, 2 raisins at 84 centimeters, present. Each line represents means of birds tested three times but in different orders, as indicated. Redrawn from Shafir, Waite, and Smith (2002) with permission.

other (e.g., equally large but more costly; see Figure 11.11) increases choice of the target relative to the competitor (i.e., T/T+C increases; the *asymmetrically dominated decoy effect*). Similarly, in this example choices of C relative to T may increase in the presence of a more costly but equally small decoy D'. The absolute number of choices of a target may even increase in the presence of an asymmetrically dominated decoy, a clear violation of rationality which raises the question of how psychological mechanisms of evaluation could depend on context in this way. In this example (shown in Figure 11.1) one possibility is that the larger but more expensive T appears less costly when contrasted with the even more costly but equally large D.

Because most studies of animal choice present only two options while nature presents many (not always a good thing; Hutchinson 2005), these findings with people suggest it is important to discover whether irrelevant alternatives can have similar effects on other species. If they do, the next question is whether this reflects a cognitive mechanism that is optimal in some other context. In a particularly straightforward test of the effect of irrelevant alternatives, Shafir, Waite, and Smith (2002) let tame free-ranging gray jays (*Psorieus canadensis*) collect raisins to hoard from wire-mesh tubes. The birds had to hop into a tube to collect the raisins, a potentially costly activity because being inside a tube increases vulnerability to predation. The binary choice of interest was 1 raisin 28 centimeters inside one tube versus 2 raisins 56 centimeters inside another; the decoy was 2 raisins at 84 centimeters. During blocks of trials with the decoy, choices of 2 raisins at 56 centimeters rose not only in relative but also in absolute terms. As Figure 11.11b indicates, this effect appeared in two separate groups of birds for which binary and trinary choices were administered in different sequences. It is apparent even when the two groups of birds are compared in the third test, by which time all of them had had the same experience and presumably hoarded about the same number of raisins.

The gray jays in this study could immediately perceive the options, like human consumers or people in experiments who only need to be told them. When animals have to be trained more extensively, the options at different stages of the experiment may change energetic state in ways that by themselves influence preference. This was demonstrated in an elegant experiment by Schuck-Paim, Pompilio, and Kacelnik (2004) in which starlings chose between pecking keys that signified 5 food items delayed 10 seconds versus 2 food items delayed 4 seconds. Notice that short-term E/T is the same for both options, that is, 1 item per 2 seconds, so there is no particular reason to prefer one or the other. However, because choices were separated by a 1-minute intertrial interval, the 5 item/10 second option gave the higher rate of intake over an experimental session. Birds preferred it, though not exclusively. The decoys were 5 food items delayed 20 seconds or 1 food item delayed 4 seconds. As in some experiments reviewed earlier, short blocks of trials contained forced exposure to each of the current options followed by choice trials. Importantly, each decoy was tested in a separate series of trials that included both trinary choices and each possible binary choice. As a result the birds' overall intake was higher in sessions with the 5 item/20 second decoy than in those with the 1 item/4 second decoy. Moreover, reduced hunger by itself reduced preference for the 5-item option in a group of birds exposed only to the critical binary choice. Controlling for overall intake by giving extra free feedings eliminated any differential effect of the two decoys in trinary choices. Such effects of hunger could have been involved in previous related studies such as one with hummingbirds (Bateson, Healy, and Hurly 2003; Schuck-Paim., Pompilio, and Kacelnik 2004). Moreover, it turns out that adding options to a choice task, even if some of them are identical in value, can change preferences (Schuck-Palm and

Kacelnik 2007). As Schuck-Paim, Pompilio, and Kacelnik (2004) conclude, when adapting paradigms from economics for animals it is important to ensure the tests do not introduce extraneous variables.

Sunk costs

A person who has already put a lot of effort into trying to obtain something may act as if this goal into which so many costs have been sunk has more value than it otherwise would. In behavioral ecology such a *sunk costs* effect is called the *Concorde fallacy,* after the supersonic airliner which Britain and France persisted in building even when it became apparent that it could never be operated economically. In human psychology, overvaluing the object of a past investment is attributed to an attempt to reduce cognitive dissonance. Like the effect of asymmetrically dominated decoys, the sunk costs effect seems to be an example of irrationality: the mere fact that one has sunk effort into getting something does not increase its intrinsic value. But animals can behave in the same way (Kacelnik and Marsh 2002). Starlings completed either 4 or 16 flights across a cage like that shown in Figure 11.5. When the required number of flights was completed, a distinctively colored key lit up and one peck on it delivered a standard amount of food. When the starlings chose between the two colors on occasional trials with no preceding flight requirement, they preferred the color that had followed 16 flights. Clement and colleagues (2000) found a similar effect in pigeons with work defined as number of key pecks. Likewise, in a simple laboratory task people prefer the stimuli that follow a more effortful response, suggesting that contrast effects explain some aspects of cognitive dissonance (Klein, Bhatt, and Zentall 2005). One interpretation of such findings (Kacelnik and Marsh 2002) is that stimuli are valued in proportion to the improvement in state associated with them in the past. For example in the study with starlings, because four flights does not have a very great energetic cost, the reward is not perceived as improving the bird's state very much compared to the situation after 16 flights.

This general notion turns out to predict a variety of striking cases of "irrational" preferences between objectively identical rewards previously experienced when the subject was in different states. Both starlings (Marsh, Schuck-Paim, and Kacelnik 2004) and desert locusts (Pompilio, Kacelnik, and Behmer 2006) prefer food-related cues experienced when they were hungry. In the locusts this may occur because hunger directly modulates the perception of food. Such effects can be quite extreme: starlings that experienced a 10 second delay to food while only slightly hungry and a longer delay to the same amount of food when quite hungry preferred the stimulus associated with the longer delay, up to 17.5 seconds, whether tested hungry or sated (Pompilio and Kacelnik 2005). Pigeons prefer stimuli (secondary reinforcers) that follow the absence rather than the presence of reinforcement (Friedrich, Clement, and Zentall 2005). This and related effects can be attributed to the original experience of the relevant stimuli being associated with positive contrast (Zentall and Singer 2007), a psychological label for the positive value of an improvement in state. The way in which the psychological value of reward depends on past experience will be taken up again when we discuss incentive motivation in Section 11.3. In the present context, however, we can conclude that as with context dependent choices, research on analogues to sunk costs and similar phenomena in animals has shown that decisions with suboptimal outcomes in these contexts can result from general mechanisms of reinforcement and choice.

11.2 Long-term or short-term maximizing: Do animals plan ahead?

11.2.1 Delayed reinforcement, impulsiveness, and temporal discounting

The psychological literature on learning and choice suggests that animals seldom anticipate events more than a few seconds or minutes in the future (W. Roberts 2002). Even a small delay between response and reinforcer has a devastating effect on rate of learning (see Bouton 2007). Learning with delayed reinforcers can be improved in various ways, for example by introducing one or more stimulus changes between response and reinforcer, but the delays that can be bridged in this way are generally minutes at the most. Even the knowledge that free food will come later does not decrease rats' willingness to work quite hard for food available in the present (Timberlake 1984). In Section 11.1 we have seen other evidence of apparent insensitivity to long-term gain, for instance in the suggestion that animals choose among options on the basis of the delay to the next scheduled reward, that is, short-term rather than long-term E/T. Nowhere is this more evident than in so-called self-control experiments, experiments which in fact demonstrate exactly the opposite, namely *impulsiveness,* also referred to as *preference for immediacy* or *temporal myopia* (W. Roberts 2002).

By analogy with situations in which people might exhibit self control by, say, rejecting a beer now in the interest of a safe drive home later, subjects in experiments on self control choose between a short delay to a relatively small reward and a longer delay to a larger reward. In the typical design, diagrammed in Figure 11.12, the total durations of trials are equated across options by adjusting the delay between reward and the beginning of the next trial. Thus the long delay/large reward option gives more reward per trial and thereby maximizes intake over a session even when it gives the same E/T as the small reward/short delay option if T is measured from trial onset to reward. Most animals that have been tested strongly prefer a short/small option. For example, given the choice between 2 seconds of eating after a 2-second wait and 6

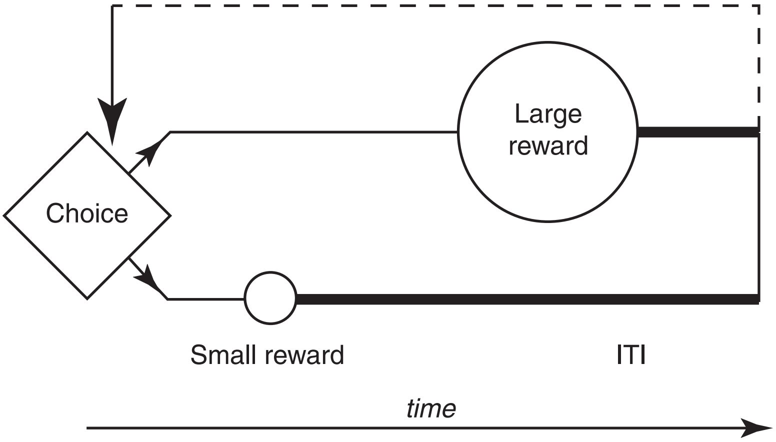


Figure 11.12. Procedure for a self-control experiment. A trial begins with a choice between a small reward after a short delay and a larger reward after a longer delay. Regardless of which is chosen lengths of trials are equated by varying the intertrial interval that separates receipt of reward from the next choice (ITI, the heavy line).

seconds of eating after a 6-second wait, pigeons and rats choose the short/small option on 97% and 80% of trials respectively (Tobin and Logue 1994), but cynomologous monkeys show self control with similar parameters (Tobin et al. 1996) as do human adults (Tobin and Logue 1994).

Although humans are not necessarily very good at delaying gratification in real-life economic situations (Fehr 2002), the dramatic failures of other species to show even modest self control (or, equivalently, patience) in laboratory tests suggests that we may be better at it than most other animals. In a direct test of this notion, Jeffrey Stevens and colleagues (Stevens, Hallinan, and Hauser 2005; Rosati et al. 2007) tested humans, marmosets, tamarins, chimpanzees, and bonobos with the delay to the larger reward titrated until a long/large option was chosen as often as an immediate/small one. Most interestingly, when chimpanzees and university students chose between two food items immediately and six items delayed two minutes, the chimpanzees chose the delayed reward on over 70% of trials, whereas the students chose it on fewer than 20% of trials. When money was substituted for food, however, the students' chose the delayed reward on nearly 60% of trials. The authors conclude from the differences between monkeys on the one hand and apes and humans on the other that "core components of the capacity for future-oriented decisions" are shared across the ape/human lineage (Rosati et al. 2007, 1663).

The effect of money versus food on humans' choices should serve as a reminder that conclusions about species differences here, as elsewhere, must be based on multiple tests. When food is involved, species differences in impulsiveness may be related to body weight, with smaller animals being more impulsive (Tobin and Logue 1994), or to feeding ecology, with animals that catch active prey like moving insects being more impulsive (Stevens, Hallinan, and Hauser 2005). The ability to delay reward may also be important in social contexts. In theory, some reciprocal social exchanges involve performing a costly altruistic act in anticipation of the favor being returned hours or days later (see Chapter 12), but the few relevant data provide little evidence that reciprocal social exchanges could be based on such self control (Stevens and Hauser 2004). For example, chimpanzees wait at most eight minutes to exchange a small piece of cookie for a large one (Dufour et al. 2007). But all the data mentioned here are from animals waiting (or not) for food. Self-control might be more evident with resources that are unlikely to disappear or be lost to competitors, such as a water hole or a safe shelter within an animal's territory.

A psychological explanation for impulsiveness is that rewards are discounted in value the more they are delayed. Discounting can be tracked in a titration procedure (see Section 11.1.4) to discover how much immediate food is psychologically equivalent to a given amount of delayed food. Consistent with self-control experiments, this procedure reveals very steep discounting functions for rats and pigeons. For example, to a pigeon food delayed 2–4 seconds is worth less than half the same amount of immediate food (Green. et al. 2004). An informal functional explanation is that psychological discounting is an adaptation to the uncertainty of the future: delayed rewards should be devalued in proportion to the probability that they will decay, be lost to competitors, or the like. As the adage has it, "a bird in the hand is worth two in the bush." But the discounting functions just described seem more extreme than any natural situation demands. One alternative explanation is that the short term rate maximization they reflect does lead to maximizing long term intake rates in natural situations, as when choosing whether to stay in a patch or move on (Stephens., Brown, and Ydenberg 2004). Thus discounting is consistent with evidence in Section 11.1 that animals can behave much as predicted by models based on maximizing long-term E/T even when responding on the basis of shorter-term currencies. In any case, none of the evidence summarized here indicates that animals anticipate events days or even hours in the future.

11.2.2 The Bischof-Kohler hypothesis and cognitive time travel

Learning and memory allow animals to behave in ways that prepare them for the future, but without any explicit representation of the future (or the past) as such. For example, conditioned responses express present knowledge about stimuli experienced in the past. Similarly, animals may respond adaptively to recurring daily or seasonal cues by migrating, hibernating, building nests, or caching food, but members of each new generation do so before experiencing the consequences of their behavior and thus presumably without foreseeing those consequences. The Monarch butterflies that fly from Canada to Mexico each fall are the grandchildren or even more distant descendents of the last Monarchs that made the trip South, and they find the wintering grounds without ever having contact with experienced individuals. Food caching bird species whose development has been studied begin to cache early in development even when hand-raised (Clayton 1994), and as adults food-storers express a compulsion to cache without regard to consequences (de Kort. et al. 2007).

Given the power of selection together with learning to produce future-oriented behaviors that do not demand interpretation as planning, what would behavioral evidence for future planning look like? This question hardly arose in comparative cognition research until recently, when Suddendorf and Corballis (1997) drew attention to a claim by Bischof and Kohler that animals, unlike adult humans, are cognitively "stuck in the present" (see also W. Roberts 2002). They dubbed this claim, that no animal engages in *mental time travel,* recreating the past and imagining the future, the Bischof-Kohler hypothesis. By itself such a hypothesis is meaningless, even empty, because we have no direct access to animals' mental events. But this consideration has not discouraged attempts to demonstrate planning for the future in nonhuman species. As with studies of animal episodic -like memory (Chapter 7), the convincingness of these demonstrations depends on how well they fit a clear set of behavioral criteria.

Suddendorf and Busby (2005) proposed that to be evidence of planning, a behavior or combination of behaviors must be novel (thus ruling out conditioned responses, migration, and the like), and it must function in the service of a motivational state other than one the animal is in at the time of performing it. For instance, like a shopper heading to the supermarket after an ample dinner, an animal that can plan would amass resources against future hunger or thirst even while sated. This criterion helps to rule out behaviors acquired or maintained through long-delayed reinforcement, assuming they would not continue without the relevant motivation. Another criterion that rules out gradual learning with delayed reinforcement is that the behavior should be shown reliably as soon as the required information is provided. Finally, planninglike behavior should not be domain-specific but be capable of being expressed in more than one context.

Even human children do not show behavior that fits all these criteria until they are four or five years old (Suddendorf and Busby 2005), but so far no other animals ever do. For instance, planning a route among familiar sites can be seen (cf. Chapter 8 and Janson 2007) as choosing among present stimuli, the cues visible from the animal's present location, which are associated with different delays, energy expenditures, and/or amounts of reward. In a study conceived as a test of the Bischof-Kohler hypothesis, Naqshbandi and Roberts (2006) allowed monkeys or rats to choose between two quantities of food, dates for the monkeys and raisins for the rats. The animals naturally preferred the larger amount, but eating so many dates or raisins at once demonstrably made the animals thirsty. To test whether they could foresee their future thirst while sated with water, they were then exposed to a regime in which water was removed from their cages when the foods were offered but returned sooner on trials when the smaller amount was chosen. With the monkeys, choice of the larger number of dates did fall after about 6 trials and in the one monkey tested it recovered when baseline conditions were reinstated. Rats did not show a comparable effect, but they showed only a weak and variable preference for the larger quantity in the first place. In any case, the fact that preference changed gradually, if at all, means this example fails the test of planning and suggests that delayed reinforcement or punishment was operating in some way.

In an experiment very much like one suggested by Tulving (2005) as a test of mental time travel for children, Mulcahy and Call (2006) tested whether bonobos and orangutans save tools for future use. The animals first learned to use a tool to get grapes from a dispenser. Then while the apparatus was blocked they had opportunity to choose one object from a collection of objects in the test room and take it to an adjoining chamber, where they waited for an hour before being readmitted to the test room with the apparatus available. All animals tested took a tool on some occasions, but their performance was very spotty. For instance, one orangutan took a tool four times in a row on the first eight trials and then not again till trial 14. An anthropocentric view point, that is, folk psychology, would seem to predict that once an animal understood that planning ahead is helpful it would plan on every trial. Moreover, in this task how often a particular tool is taken at random most likely depends on the alternative objects offered and how often they have been paired with food or otherwise used in the recent past, and this was neither well specified nor investigated here. And finally, because using the tool resulted in a treat of grapes that the animals presumably always desired, planning for a future need was not tested (Suddendorf 2006).

Somewhat stronger evidence comes from a similar study (Osvath and Osvath 2008) in which two chimpanzees and an orangutan nearly always chose a tube for sucking juice from a container an hour before opportunity to use it. Whether the animals were planning or simply taking the object most strongly associated with food was addressed by making a piece of favorite fruit one of the options. All animals still chose the tube first on at least half the trials. Moreover, when a second choice of fruit versus tube was given after an animal already had a tube, all animals chose the fruit. They also showed appropriate choice of a stick tool. A next step with studies of this kind would be to offer multiple functional tools and seek evidence that choice anticipates a specific future task. However if such behavior were found, it would be necessary to show how it was different from a conditional discrimination based on present cues to what tool can be used next.

In any case, the candidate that so far fits the largest number of criteria for planning comes not from choice of tools but from food storing in scrub jays (Raby et al. 2007). The birds in this study lived in large cages with three compartments ("rooms"; Figure 11.13). After first acquiring information about which room had food in the morning, they behaved as if planning for breakfast by caching food items in the evening where they were most likely to be needed. For example, in Experiment 1 they first experienced three cycles of a treatment in which they received "breakfast" of pine nuts in the morning in one end room; in the other end room, no breakfast was

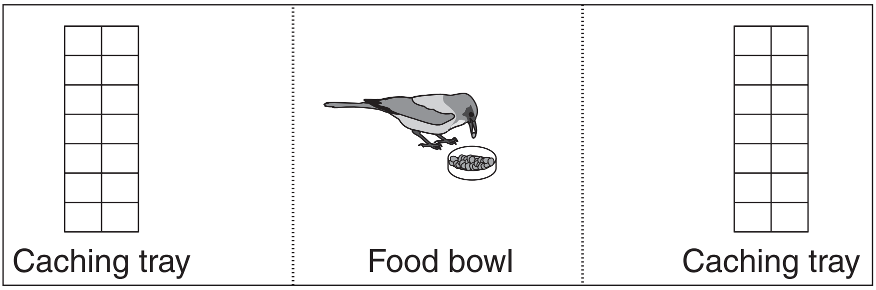


Figure 11.13. Diagram (not to scale) of the setup used by Raby et al. (2007) to test future planning in scrub jays. Seeds were in the food bowl and the caching trays present in the end "rooms" in the evening only for the final test. Otherwise uncachable powdered food was in the food bowl in the evening and the birds were closed into one room or the other for the night, where they either had breakfast or not in the morning. After Raby et al. (2007) with permission.

provided until 2 hours after daylight. In the test, for the first time whole pine nuts were provided in the central room in the evening along with sand-filled trays for caching in the two end rooms. The birds cached three times as many pine nuts in the "no breakfast room" as in the "breakfast room." Importantly, all the data came from this first test, before the birds had experienced the consequences of their choices. Similarly, birds learned to expect breakfast in both rooms in the second experiment, peanuts in one and dog kibble in the other. On their first opportunity to cache peanuts and dog kibble in the evening, they distributed their caches so as to provide each room with more of the food it usually lacked.

Although this study was greeted (e.g., by Shettleworth 2007) as an advance over earlier ones with primates, it lacks a control for the possibility that scrub jays were expressing a natural tendency to spread out caches of a given food type irrespective of information about how this would determine what they had to eat the next day (Premack 2007; Suddendorf and Corballis 2008b; but see Clayton. et al. 2008). For an animal that caches different kinds of items (and that, as we saw in Chapter 7, can remember what it cached where), a strategy of distributing items of each type as widely as possible would help to defeat predators that might raid just one of those types. In any case, the birds' hoarding here is not clearly behavior for a future need because although they could both eat and cache during the test they may have been somewhat hungry. Correia and colleagues (Correia, Dickinson, and Clayton 2007) used stimulus-specific satiety to address this issue. Birds were sated on one of two foods, peanuts or dog kibble, by prefeeding them with it just before opportunity to cache both foods. Such prefeeding selectively suppresses not only consumption but caching of the prefed item. Here, however, some birds were additionally prefed the alternative item just before opportunity to recover their caches. If they could foresee that they would not want this item at the time of retrieval, they should suppress caching of it initially rather than of the item they were just prefed. Although the findings of this study appear under a title proclaiming positive results, the birds cached so little in the test trials, some of them not at all, that the best conclusion here is "provocative but not proven." Moreover, even if more substantial data were consistent with those published so far, they can be interpreted as a novel and subtle adaptation of the food-hoarding system rather than evidence for a more domain general "mental time travel" (Premack 2007; Suddendorf and Corballis 2008b).

As with episodic memory (Chapter 7), an important impetus for the set of studies reviewed here is the wish to understand the neural substrate of human mental time travel. Mentally recreating the past and imagining the future turn out to share neural underpinnings in normal adults, and patients with impaired episodic memory may also have difficulty thinking about the future (Addis, Wong, and Schacter 2007). None of this seems very surprising. Both conscious and unconscious memory presumably were selected in the first place because they allow past experience to influence future behavior. Indeed, it seems plausible that the adaptive value of episodic memory, in the sense of "mental time travel" into the past, lies entirely in allowing its possessor to imagine and thus plan for the future. Autonoetic consciousness and concomitant future planning may indeed be uniquely human (Suddendorf and Corballis 2008a), but other animals clearly share with humans multiple kinds of future-oriented behavior (W. Roberts et al. 2008; Raby and Clayton 2009). Notwithstanding the challenge laid down by the Bischof-Kohler hypothesis, a more productive way forward may be to look for the components of planning, which species show them, and under what conditions (Raby and Clayton 2009).

11. 3 Causal learning and instrumental behavior

11.3.1 Theories of instrumental learning

Just as a bird storing food looks as if it is planning, an animal performing an instrumentally trained activity such as a rat pressing a lever gives a compelling impression that it "knows what it is doing." Only recently has evidence been sought (and found) that this is more than an impression. This section is about the causal knowledge underlying activities like rats' bar pressing. It will provide a context for analyses of tool using in Section 11.4, but first a little history is in order.

The Skinnerian or behavior analysis approach to operant conditioning, many findings from which have appeared earlier in this chapter, was largely atheoretical. It was and still is (see Staddon and Cerutti 2003) the descriptive study of behavior's control by the environment, particularly as instantiated by schedules of reinforcement. Traditionally, however, beginning with Thorndike (1911/1970) instrumental performance was thought to reflect S-R learning: responses become connected to situational stimuli through the stamping in action of reinforcement. This account provides no role for a representation of the reinforcer in instrumental performance; in an important sense an S-R animal does *not* "know what it is doing." But, as discussed more in a moment, performance of an instrumental action can be modulated by information about the current value of its reinforcer. Moreover, although the S-R account suggests that mere contiguity with a reinforcer suffices to stamp in a response, the reinforcer needs to be contingent on the response just as a US needs to be contingent on a CS for Pavlovian conditioning (Chapter 4).

In an elegant demonstration of this principle, Balleine and Dickinson (1998) trained rats to press a lever for one of two reinforcers, food pellets or starch solution, and in separate sessions to pull a chain for the other reinforcer. When the rats were performing both responses at high rates, the contingency between one response and reinforcement was degraded by introducing free presentations of its reinforcer. For example, a rat trained to pull the chain for pellets would receive additional pellets at times when it had not just pulled the chain while its lever-pressing sessions continued normally. Response rate gradually fell almost to zero for the response whose contingency was degraded whereas it remained high for the alternative response. This effect depended on the extra reinforcers being the same as the normal reinforcer for the response in question. Thus rats pulling the chain for pellets continued to pull when given noncontingent starch reinforcers.

The foregoing findings would be expected if associative learning is a general mechanism for learning simple causal relationships between events regardless of their nature, and indeed, animals learn response-reinforcer associations through the same laws of learning as in Pavlovian conditioning (Mackintosh 1983; Dickinson 1994). But this can make it difficult to know whether behavior in an instrumental conditioning experiment is in fact the expression of instrumental learning. Operationally the distinction between Pavlovian and instrumental conditioning is perfectly clear: in Pavlovian conditioning the experimenter arranges a contingency between a relatively neutral stimulus and a reinforcer; in instrumental conditioning, the contingency is between some aspect of the animal's behavior and a reinforcer. However, any instrumental conditioning setup inevitably includes external stimuli, and a resulting Pavlovian contingency could be what actually controls behavior. For instance, when a rat is reinforced with food for running down a runway, does it run because the act of running predicts food or because running is the CR (i.e., approaching) resulting from associations between stimuli at the far end of the runway and the food found there? Key pecking by pigeons, an archetypal Skinnerian operant, turns out to be a Pavlovian CR that develops from experience of a key light—food contingency (i.e., in autoshaping, see Chapter 4). Furthermore, if the food is omitted each time the bird pecks but presented after each lighting of the key without pecks (an *omission procedure*), pigeons peck anyway, though less than without omission (D. Williams and Williams 1969).

One way to be sure that performance of a particular response is free of Pavlovian influences is to show that both the response and its opposite—for example pushing a lever up and pushing it down—can be trained by making a given reinforcer contingent on them. This is true, perhaps uniquely, of lever pressing in rats (Dickinson and Balleine 2000). Accordingly, the cognitive structures underlying instrumental performance have been most thoroughly analyzed using this and similar responses (Dickinson and Balleine 1994, 2000). The results of this analysis suggest that instrumental performance can be understood as an inference from the information contained in a response-reinforcer association together with information about the current value of the reinforcer. In effect, bar pressing reflects both a belief "bar pressing causes food" and a desire for food. Belief is induced by experience of the response-reinforcer contingency. Desire is surprisingly less straightforward, as discussed next.

11.3.2 Instrumental incentive learning

In Section 4.5.1 we saw that when a food US is revalued after Pavlovian conditioning by pairing it with poison or by changing the animal's hunger for that food, CRs to the CS signaling that food change accordingly. Similar effects are observed in instrumental conditioning. For example, Colwill and Rescorla (1985) trained individual rats to both pull a chain for sucrose and press a lever for food pellets (or the reverse pairings). The rats were then made ill after consuming one of the reinforcers in their home cages. In a subsequent test during extinction they immediately reduced their rate of performing the response that had previously gained the now-undesirable reinforcer (figure 11.14). At the beginning of the test the belief that a particular

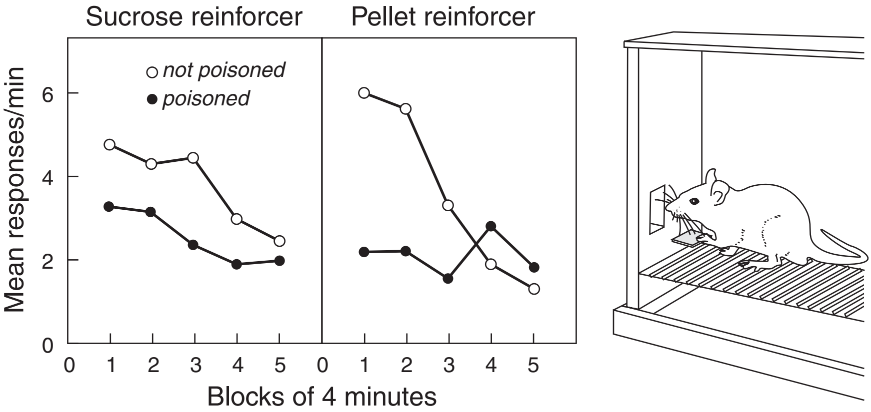


Figure 11.14. Results of the final, extinction, stage of an experiment demonstrating response-reinforcer associations in instrumental learning. Different groups of rats, each trained to make one response for sucrose and another for pellets, had experienced mild poisoning following ingestion of either sucrose or pellets and were tested in extinction. Redrawn from Colwill and Rescorla (1985) with permission.

response gave a particular food was intact (although the absence of any food soon changed that), but rats no longer desired the poisoned food. Notice that testing in extinction revealed the representation that controlled pressing originally; any reduction in responding could not reflect new learning that one response led to a disgusting food. Notice, too, that responding for the poisoned reinforcer was not entirely abolished, at least when the reinforcer was sucrose (see also Dickinson et al. 1995). Residual responding in experiments of this kind is evidence of S-R learning, and it is greater following greater amounts of training. Overtrained responses become habits, independent of the value of their original reinforcer.

In Pavlovian conditioning, revaluation effects resulting from pairing a US with poison or changing the animal's motivation appear immediately. In instrumental conditioning, however, they depend on past experience with the reinforcer, experience that leads to *instrumental incentive learning* (Dickinson and Balleine 1994, 2002). Animals have to experience the changed hedonic value of a reinforcer before responding for it changes appropriately. For example, in experiments like that of Colwill and Rescorla (1985) in the poisoning phase it is important to have multiple trials during which rats taste the food after it has become undesirable (see Dickinson and Balleine 2002). Remarkably, hunger and satiety work in the same way. In an elegant demonstration, Balleine (1992) trained rats to bar press for food pellets while somewhat sated and then tested different subgroups in extinction while they were either hungry or sated. Hungry rats pressed more than sated rats only if they had previously consumed pellets when they were hungry. Similarly, rats trained when hungry reduced their response rate when sated only after prior exposure to the food reinforcer in the sated state. Like the revaluation resulting from poisoning, these effects are specific to the foods eaten in the relevant state (Balleine 1992; Dickinson and Balleine 2002). On one view (Dickinson and Balleine 2000; Dickinson 2008) this instrumental incentive learning relies on a primitive form of phenomenal consciousness, namely awareness of the hedonic value of the reinforcer. This combines with causal knowledge about the response-reinforcer relationship (in effect, the rat's belief that pressing causes food), to generate responding. This interpretation implies that experience with associative relationships results in connections that are more than excitatory or inhibitory links between representations but rather themselves have representational content, a possibility investigated next.

11.3.3 Reasoning and causal learning

As we have seen in Chapter 4 (and see Rescorla 1988a), although associative learning can be viewed as an adaptation for acquiring causal knowledge, that is, some representation functionally equivalent to "A causes B," this need not mean animals represent causation as such. The effects of conditioning can be modeled as excitatory and inhibitory connections between event representations. Some, but arguably not all, human causal learning is well described by the same associative models discussed in Chapter 4 (Shanks 1994; Dickinson 2001b; Penn and Povinelli 2007a). However, the reasoning evident in deducing relationships among events in daily life or conducting scientific experiments seems to encompass an understanding of the nature of causes as such. Such causal understanding and how it develops has become an active area of research in cognitive and developmental psychology (Gopnik and Schulz 2004; Gopnik and Schulz 2007). One simple illustration of qualitatively different kinds of causes ("causal models" in terms of this literature) is depicted in Figure 11.15 (Waldmann, Hagmayer, and Blaisdell 2006). In the scenario on the top left, two fictitious hormones ("sonin" and "xanthan") have a common cause in a third one

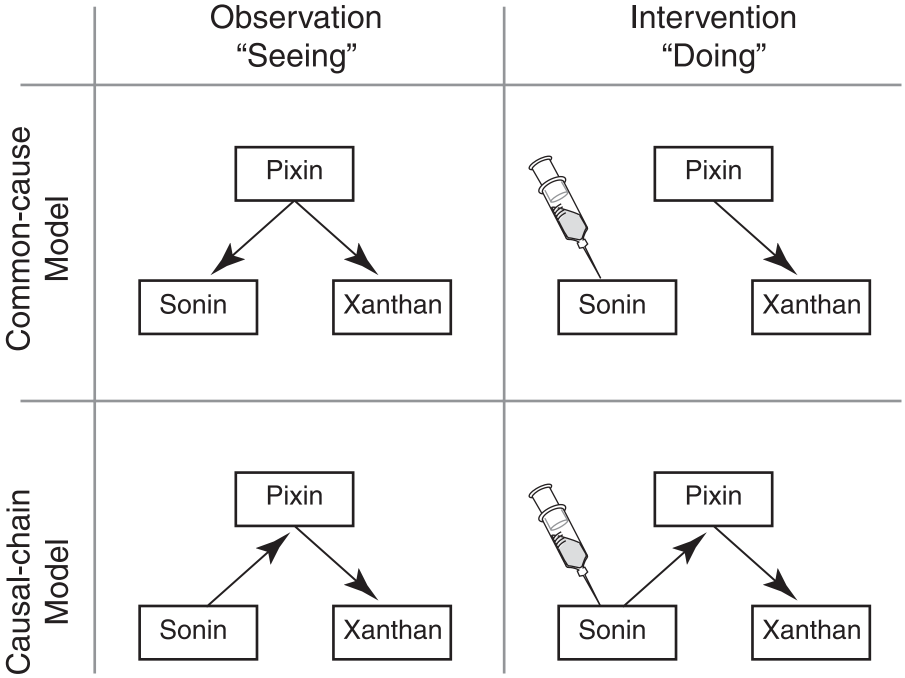


Figure 11.15. Tests of two kinds of causal reasoning by humans. Subjects are exposed to the causal relationships among fictitious biochemicals depicted on the left and then asked whether "xanthan" will be present when "sonin" is injected, as represented on the right. After Waldmann, Hagmayer, and Blaisdell (2006) with permission.

("pixin"). Therefore, if one intervenes by injecting sonin, xanthan should not be present (top right). In contrast, if the same three hormones are part of a causal chain (bottom left) such that sonin causes release of pixin which in turn causes release of xanthan, the same intervention should lead to the presence of xanthan. People do understand the difference between a causal chain model and a common cause model, as evidenced when they are exposed to one of the relationships on the left of Figure 11.15 and then asked whether they expect xanthan to be present following intervention with sonin (Waldmann., Hagmayer, and Blaisdell 2006).

Blaisdell and colleagues (2006) devised a clever arrangement for testing whether rats behave in an analogous way. "Common cause" rats first learned through Pavlovian conditioning that a light could be followed by ("cause") either a tone or food. In the "intervention" phase, pressing a novel lever produced the tone. These rats should not expect food when hearing the tone because the light had not occurred, at least if we assume the separate light-tone and light-food pairings did not induce an association between tone and food. In contrast, rats that had learned a tone-light-food causal chain should expect food when their bar-pressing produced the tone. Expectation of food was measured by the number of times the rat poked its head into the opening above the food hopper during the 10-second tone. As predicted, the "causal chain" rats poked more, as if they understood that their action should cause food to appear, whereas the common cause rats understood that their action was unlikely to cause food. Additional groups in this and related experiments (Leising et al. 2008) successfully controlled for obvious alternative explanations such as differences in how recently the various elements of prior learning had been acquired.

Research on analogues to reasoning in the context of conditioning-like paradigms is still relatively new. There are candidates in purely Pavlovian paradigms, too (Beckers et al. 2006; Penn and Povinelli 2007a). Even if claims that these findings defy explanation in terms of established models of associative learning withstand additional scrutiny, the mechanism involved remains to be specified (Waldmann. et al. 2008). Models such as those depicted in Figure 11.15 are normative, that is, abstract functional descriptions of causal reasoning. Findings like those of Blaisdell, Leising, and Waldmann (2006) open the question of how experience induces behavior that approximates their outputs. What, if anything, is involved beyond networks of excitatory and inhibitory connections?

But why might such a reasoning-like process have evolved in an animal sometimes referred to (e.g., by Dickinson 2008) as "the humble rat"? Do any natural situations require discriminating between interventions in causal chains versus common cause models? Some suggestions come from Tomasello and Call's (1997, Chapter 12) discussion of the limits to primates' causal understanding, where they imagine scenarios that require reasoning about interventions after observing causal chains. Importantly, Tomasello and Call conclude that primates would be very unlikely to make what to people are obvious deductions. For example, when an animal sees the wind shaking a branch and causing fruit to fall, why does it not reason "I could shake the branch myself to get fruit"? Similarly, if an animal sees a rock fall down a slope and cause a group of its conspecifics to scatter, why does it not reason that it could roll a rock to drive competitors away from some desired resource?

The structure of these situations resembles that of an instrumental secondary reinforcement experiment in which pairings of a CS with food increase a response that produces the CS (as in the control condition in Blaisdell et al. 2006). One difference is that in the scenarios described by Tomasello and Call "reasoning" would consist of spontaneous inferences about one's own behavior based on experience in the past rather than acquired in the situation at hand. These scenarios also resemble tests of the ability to copy another's actions. For example, suppose animal B sees animal A rather than the wind shaking the fruit-laden branch. As we learn in Chapter 13, most animals are not very good imitators, that is, given this experience they would not shake the branch themselves. Tomasello and Call suggest that reasoning about the shaking branch or the rolling rock requires understanding *why* causes have their effects. The latter case, they suggest, involves understanding the minds of conspecifics, a matter taken up in Chapter 12. The former involves physical understanding, the topic of the next section. Both require in some sense interpreting sequences of events as the results of unseen causes (thoughts and emotions of others; gravity and other physical forces). On one compelling and forcefully stated view (Povinelli and Vonk 2003; Vonk and Povinelli 2006; Penn and Povinelli 2007a), this kind of causal understanding is unavailable to species other than humans.

11. 4 Using and understanding tools

Tool use has been defined as "the use of an external object as a functional extension of mouth or beak, hand or claw, in the attainment of an immediate goal" (van Lawick-Goodall 1970). Making and using tools is often seen as a landmark in human evolution, but in fact all sorts of animals use tools (Beck 1980). Some crabs attach anenomes to their claws, where the anenomes' stings repel the crab's enemies. Sea otters break mollusk shells on stone "anvils" that they hold on their chests. Egyptian vultures crack ostrich eggs by throwing stones at them, and chimpanzees use bunches of leaves as sponges to collect water from crevices. Some animals make the tools they use. New Caledonian crows nibble strips off the stiff edges of pandanus leaves and use them to extract insects from holes (Hunt 1996; Bluff et al. 2007; see the cover of this book for a photograph of one of these crows with a twig tool). Chimpanzees make a variety of tools from sticks, leaves, and grass (McGrew 1992; Whiten et al. 2001).

As a functional category of behavior, tool use is hazy around the edges (St Amant and Horton 2008). For instance, only from an anthropocentric viewpoint does it make sense to distinguish one gull's dropping stones onto mussels (tool use) from another's dropping mussels onto stones (not tool use, see Beck 1980, 1982). Both are performing a food-reinforced chain of behavior involving stones. And to take another avian example, New Caledonian crows' ability to choose appropriate materials for tools and manipulate them to extract food from holes is arguably less impressive than the discriminative and motor skills shown by myriads of other bird species in building their nests (Hansell 2000). But in humans, using tools is also thought to entail at least an implicit understanding of how and why tools work, a simple "folk physics." Furthermore, like early hominids, chimpanzees in different geographic areas have distinctive types and uses of tools (Whiten et al. 2001) suggesting that tool use is transmitted socially and, more controversially, that apes have a primitive form of culture (Chapter 13). Provocative terms like "folk physics for apes" (Povinelli 2000) and "chimpanzee cultures" (Whiten et al. 2001) have attracted attention to animal tool use, and new findings about tool use by birds have increased it. Alongside of field work, clever laboratory analogues of situations observed in the field have been devised to allow a critical, controlled, look at two complementary questions. (1) How is tool use acquired? Is it, as might appear to the skeptic, entirely instrumental learning by trial and error or is some form of social influence required? Is insight ever involved? (2) What do animals understand about tools? Do they, for example, immediately recognize—in a way not explicable as stimulus generalization from past experience—what tool is needed in a given situation? We begin, however, with a brief look at the evolution and function of tool use.

11.4.1 What kinds of animals use tools?

Hundreds of observations of primates (Reader and Laland 2002) and birds (Lefebvre, Nicolakakis, and Boire 2002) using tools have been reported, not to mention candidates from other taxa, but routine use of genuine tools by one or more populations is established for only two species of birds and a few primates. A "genuine" tool is one the animal manipulates, like a stick used to extract prey from holes. "Borderline tools" (Lefebvre., Nicolakakis, and Boire 2002) are objects that are used but not actually manipulated, like the balls of mammal dung that burrowing owls place around their nests to attract the beetles which they eat (Levy, Duncan, and Levins 2004). One obvious ecological prerequisite for using genuine tools to get food is that the animal rely to some extent on *extractive foraging,* that is, eating things that have to be extracted from a hard shell or a hiding place inside a tree trunk or the like. Thus the fact that gorillas feed primarily on leaves probably accounts for the apparent rarity of tool use in this species compared to chimpanzees and orangutans (but see Breuer, Ndoundou-Hockemba, and Fishlock 2005). Among birds, it is noteworthy that the two species showing most widespread use of tools for extractive foraging, New Caledonian crows and woodpecker finches, are island species. For example, the woodpecker finch of the Galapagos does with twigs and cactus spines what a woodpecker does with its bill. Presumably in a mainland habitat it would be outcompeted by species equipped with stout bills for extracting the same kinds of prey more efficiently. The absence of competitors may open up a niche that can be exploited by evolving a behavioral specialization.

Differences among populations of tool-using species also provide some clues to ecological conditions favoring the evolution of tool use. A prime example comes from capuchin monkeys (*Cebus* species). Although capuchins readily make and use tools in captivity, researchers in the forests of South America had seldom seen them using tools in the wild (Visalberghi and Fragaszy 2006). But it turns out that several groups of these monkeys in more arid, open, areas in northeastern Brazil routinely use stones to crack nuts (Waga et al. 2006). Some groups carry hard palm nuts to habitual "anvils," where heavy stones are left lying around; a monkey may stand up bipedally holding a stone a quarter of its own weight and drop the stone onto a nut (Fragaszy et al. 2004). The reasons why these populations use tools so much more than the forest monkeys probably include both the scarcity of foods other than palm nuts and the fact that the low density of trees means the monkeys spend a lot of time on the ground, where a stone, a nut, and a hard surface are more likely to be encountered together and to remain together through repeated nut-cracking attempts than in a tree (Waga et al. 2006).

Mainly because tool making and using was traditionally assumed to be uniquely human, it is widely assumed to require some kind of exceptional cognitive ability. In any case, activities such as appropriately bringing together nut, anvil, and stone tool or selecting and modifying sticks to make a tool of a required length and thickness seem unusually cognitively demanding. These considerations suggest that tool use should be associated with enlargement of the brain or some part of it. Comparative surveys of both birds (Lefebvre, Nicolakakis, and Boire 2002) and primates (Reader and Laland 2002) have indeed found evidence for such associations. For example, correcting for such confounds as overall frequencies of observation (see Box 2.2), genuine tool use in birds has been reported most often in corvids, other passerines, and parrots, groups among those with the largest relative neostriatum and whole brain. "Borderline" tool use is related more to overall innovation rate but not to brain measures. In primates, tool use, innovation (see Box 2.2), and social learning are all related to size of the "executive brain," that is, neocortex and striatum. Neither of these surveys provides much insight into precisely what neural specialization, if any, is associated with tool using nor do they look at differences among closely related species that differ in their propensity to use tools. In any case, whether or not it requires a specialized conceptual ability, using tools might not be expected to be associated with a single localized neural specialization because it can involve perceptual, motor, and/or learning abilities.

11.4.2 What do tool users understand?

Understanding what? The trap tube as a case study

A foot-long horizontal transparent tube with a peanut in the middle was placed in the cage of a group of four capuchins. When sticks were provided, monkeys used them to obtain peanuts by inserting a stick into one end of the tube and pushing the peanut out (Visalberghi and Trinca 1989). To use sticks effectively, the monkeys need not have understood anything about the requirements of the situation, such as needing a stick neither too thick nor too short and an unbroken surface between the peanut and the exit from the tube. On the face of it, poking a stick into the tube is instrumental behavior reinforced with food and acquired through trial and error. To test whether the animals understood anything other than "pushing the tool into the tube causes food," Visalberghi and her colleagues gave the capuchins clever modifications of the tube task. In what has become a benchmark test for understanding of tools, a trap was introduced in the middle of the tube (Figure 11.16, Visalberghi and Limongelli 1994). Now inserting the stick at the end closer to the reward (a candy in this experiment) pushed the reward into the trap. Three out of four capuchins given the trap tube never got the candy more than half the time in 140 trials. The fourth began to succeed almost every time after 90 trials. This individual was then given further tests designed to probe what it had learned. For instance, the tube was rotated so the trap was on top. Now the stick could be inserted on either end, but the monkey persisted in carefully selecting the end farther from the candy and frequently monitoring the movement of the candy as she slowly slid the stick into the tube. Thus this successful animal was using a distance-based associative rule.

Five captive chimpanzees were tested similarly to the capuchins (Limongelli, Boysen, and Visalberghi 1995; also see Povinelli 2000). These animals, experienced in a variety of laboratory tasks, all used sticks to get rewards from the plain tube right away. However, in 140 trials with the trap tube, only two of them ever performed above chance, and that not until after 70–80 trials. To see whether they were using a distance-based rule, these two animals were tested with a new trap tube that had the hole displaced from the center so that inserting the stick on the end nearest the reward could push it into the trap. Both animals were successful in this task almost from the beginning, showing that they took into account the position of the reward relative to the trap.

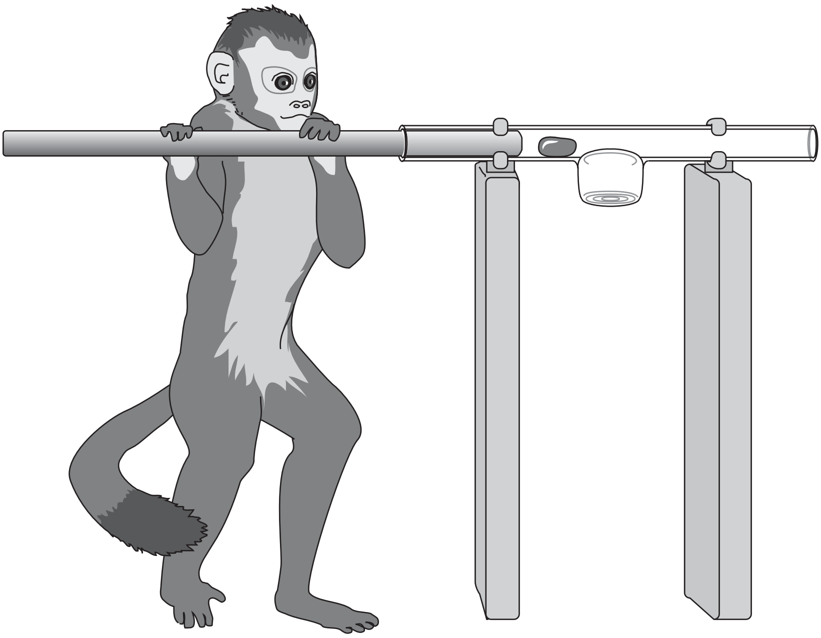


Figure 11.16. A capuchin monkey about to make an error in a trap tube task. After a photograph in Visalberghi and Limongelli (1994) with permission.

One of the successful chimpanzees anticipated the effects of the stick on the reward, as she rarely even began by inserting it on the wrong side. The other animal was more likely to begin with the stick on the wrong side, then withdraw and reinsert it. Still, these behaviors can be seen as reflecting learned rules based on the position of the reward relative to the hole, something like "Insert the stick on the side of the trap away from the candy" or "Push the stick only if it is moving the reward away from the trap."

By now, in addition to capuchins and chimpanzees, other great apes (Visalberghi, Fragaszy, and Savage-Rumbaugh 1995; Mulcahy, Call, and Dunbar 2005), several other primates (Santos et al. 2006), human children (e.g., Horner and Whiten 2007), woodpecker finches (Tebbich and Bshary 2004), a New Caledonian crow (Bluff et al. 2007), and—for good measure—human adults (Silva, Page, and Silva 2005; Silva and Silva 2006) have been tested on the trap tube task or variants of it. For example, in the "trap table task" (Povinelli 2000; Santos et al. 2006) an animal chooses between two tools for pulling food across a table toward itself, one of which is positioned to draw the food into a hole (Figure 11.17). Only human adults and children above the age of 4 or 5 immediately avoid the trap (Silva and Silva 2006; Horner and Whiten 2007). Individuals of other ages and species eventually learn to avoid it but take about as many trials as the capuchins. As suggested in the description of the successful capuchins and chimpanzees in the original studies, animals can learn to use any of a number of cues to avoid the trap. Nothing requires that they "understand gravity" or even the necessity to avoid holes or make the reward slide over an unbroken surface.

Beyond the trap tube

A serious problem here is that presenting successful animals with a tube with the trap rotated to the top is a test with very limited power. Understanding that the tube is no

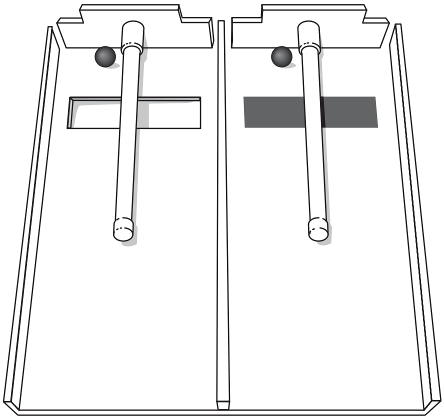


Figure 11.17. The trap table task. The subject, who would be positioned at the bottom of this figure, chooses between two rakelike tools, one of which (on the left here) will pull the reward into a trap. The alternative pulls the reward across a similarly-sized solid rectangle. After Povinelli (2000) with permission.

longer functional would be evidenced by inserting the tool at random on either end, but the same behavior would result from generalization decrement, that is, treating the altered tube as part of a new problem. More importantly, there is no cost to choosing a particular side when the trap is on top because the reward comes out regardless (Machado and Silva 2003). Indeed, unless it brings the reward sooner, human adults avoid using a tool near a nonfunctional trap, as if unthinkingly applying an algorithm "avoid traps" (Figure 11.17; Silva, Page, and Silva 2005; Silva and Silva 2006). Just as with other sorts of concept learning (Chapter 6), what is needed is a test in which conceptual understanding (here of the physical causal structure of the situation) predicts an outcome opposite to that expected from reliance on familiar cues (Machado and Silva 2003).

A design which does this was pioneered by Seed, Tebbich, Emery, and Clayton (2006), who trained rooks to avoid traps in the setups labeled A and B in Figure 11.18. Because rooks do not naturally use tools, the stick "tool" was preinserted into a tube and the birds had only to pull on the correct end to

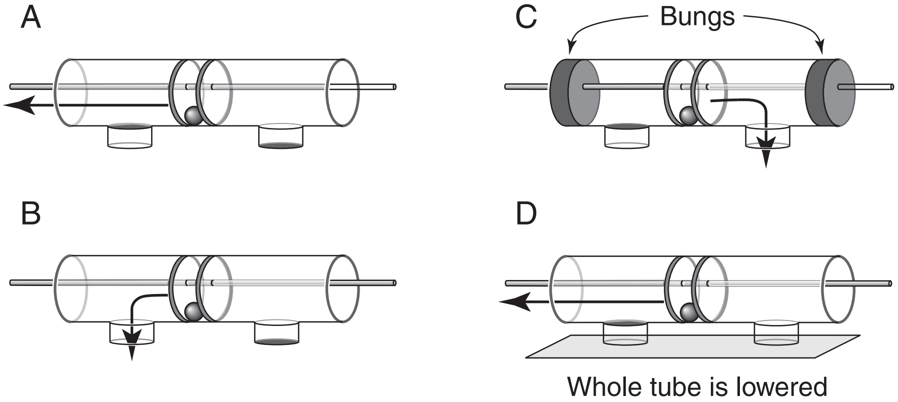


Figure 11.18. Trap tubes presented to rooks by Seed et al. (2006). Notice that in both A and B, pulling the stick to the left will release the reward. Tubes C and D each combine the "safe" ends of Tubes A and B, but require pulling in opposite directions as indicated. After Seed et al. (2006) with permission.

obtain the reward. Animals trained to a criterion of 80% correct on tube A or tube B immediately performed at a similarly high level on the other tube of the pair. However, because the trap looks the same in both cases this finding tells us only that the birds had learned to pull on the side away from the trap. Whether they had also learned something about the characteristics of traps was tested with tubes C and D. Each of them incorporated the "nontrapping" sides of tubes A and B, but arranged in such a way that success required taking into account how the reward would move when the stick was pulled. Six of 7 birds performed at chance on 20 trials with each of these tubes, but one performed almost perfectly from the outset.

What the successful rook had learned was not probed further, but a similarly designed task was used with chimpanzees (Seed et al. 2009). Initially these animals didn't use a tool but learned to slide a reward toward the exit from a transparent "trap box" by pushing it along with a finger. Training on two tasks was followed by tests in which responding based on cues predictive of success in the initial tasks were opposed to responding based on understanding traps. The animals learned both initial tasks much more quickly than previous animals required to use tools in tasks with traps, but as with the rooks only one subject (here, out of six) showed immediate transfer to the probe tasks. Then seven experienced animals along with eight naive animals were given a new version of the trap box to be used with a stick tool or a finger. This turned out to be difficult for naive animals: only one, using a finger, performed above chance in 150 trials. All experienced animals using a finger solved it within 30 trials, and two who had to use a tool also solved it within the time allowed.

This experiment supports two primary conclusions. One is that under some conditions chimpanzees apparently learn more than responses to arbitrary cues, as evidenced by the superior performance of the experienced animals in the final task. They may represent something about the functional properties of such things as a solid shelf or a barrier which allows them to transfer to new tasks with the similar elements. Notice this is not the same as understanding *why* these properties are important in terms of gravity or the tube. Here transfer to the second set of tasks was probably facilitated by the fact that the experienced chimpanzees had already learned four versions of the trap box. As we saw in Chapter 6, a concept or category is taught by exposing subjects to multiple exemplars, and this has rarely been done in other studies of tool use (Machado and Silva 2003). Indeed, a study with just two tasks, a trap tube and a "trap platform," found no evidence of transfer (Martin-Ordas, Call, and Colmenares 2008).

The second conclusion is that whether apes can succeed in avoiding traps while getting food may depend on how the task is presented. Tasks that test the same conceptual ability from a human viewpoint may make different cognitive demands on a chimpanzee. A finger may be easier to use than a stick because attending to movements of a stick leaves fewer resources for other aspects of the task (Seed et al. 2009). Similarly, choosing to rake in food from the solid side of a table with a trap is very much easier when a single tool is positioned in the middle of the table and subjects choose only where to direct it than when there is a tool on each side (as in Figure 11.17) and subjects choose which to pull (Girndt, Meier, and Call 2008). Indeed, with a single rake apes that failed a two-rake version chose the side without the trap on about 80% of trials from the very beginning. Again, a difference in attentional demands may be involved. When two rakes are positioned around food, the animal must inhibit its tendency to grab one before noting the relationship of the food to the trap (Girndt, Meier, and Call 2008). Finally, avoiding a trap may be easier when raking food than when pushing it out because pulling food toward oneself is more natural (Mulcahy and Call 2006b). Demonstrations that such conceptually irrelevant factors can be crucial have two interpretations. On the one hand, under the "right" conditions apes can solve tasks with traps much more readily than first appeared (e.g., in Povinelli 2000). On the other, if apes understood the task, these details should not matter so much. There are, however, some reasonable mechanistic explanations of why one versus two tools or the need to use any tool affects performance. The next step will be to put these explanations to the test.

What makes a good tool? Shape, size, and contact

Less demanding and arguably more central to tool use in general than avoiding traps is to discriminate between objects that are good and bad tools in the first place (Fujita, Kuroshima, and Asai 2003), for example matching the shape, thickness and/or length of tools to task requirements. In one test of this ability, capuchins, chimpanzees, bonobos, and an orangutan were given food in a tube and sticks tied into a thick bundle or a stick with smaller sticks inserted into its ends, in an *H* shape (Visalberghi, Fragaszy, and Savage-Rumbaugh 1995). All the animals untied the bundle or removed one of the small sticks from the *H* but only the apes appeared to do so out of an ability to anticipate the results of their actions. For example, the capuchins sometimes tried to push the whole bundle of sticks into the tube, but the apes never did. Two New Caledonian crows chose a stick from a "toolbox" to use for extracting meat from a transparent tube. They often took the longest stick available, which worked every time, but on trials when they did not, the length taken matched the length required pretty well. And when accessing meat through a small hole in a tube, the crows removed twigs from a branch to make a tool of the appropriate width, only rarely trying one that was too thick (review in Bluff et al. 2007). Woodpecker finches, however, often tried a stick that was too short before taking a better one from a "toolbox," but this is not so different from what they do in the wild (Tebbich and Bshary 2004). In any case, visually matching length of tool to depth of hole may have no function in the wild because the prey is usually concealed in the dark hole. This may explain why two wild New Caledonian crows offered grubs at different depths in experimenter-made visible holes behaved much like the woodpecker finches (Hunt, Rutledge, and Gray 2006).

Another test of the ability to choose good tools on the basis of their immediately perceptible characteristics is *the support problem,* a classic test of physical understanding first used by Piaget (see also Box 11.2). Very young children recognize that an out-of-reach object resting on (i.e., supported by) a cloth can be obtained by pulling on the cloth. In the version for monkeys and apes with options like those depicted in Figure 11.19 the animal chooses which of two cloths to pull to obtain an apple. An effective cloth can be perceived immediately as one with an unbroken surface, however irregular, between the working end and the treat. Cotton-top tamarins learn to discriminate between broken and unbroken cloths, even when the differences between them are quite subtle (Hauser, Kralik, and Botto-Mahan 1999). However, in tests focused on the relationship between the goal object and the cloth, chimpanzees do not immediately discriminate between cloths that actually support an object and those which simply surround or touch it, as in the examples in Figure 11.19 (Povinelli 2000).

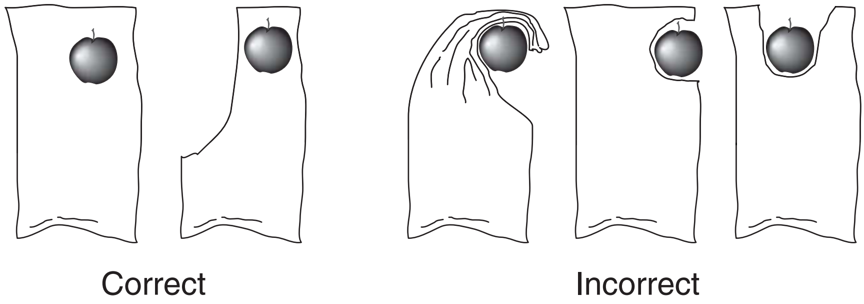


Figure 11.19. Stimuli used for testing chimpanzees on the support problem. As in the task in Figure 11.17, animals had a choice between an effective "tool" for pulling in reward such as one of the Correct options here, and an ineffective one such as the cloths on the right which surround or touch the apple but do not support it. After Povinelli (2000) with permission.

Box 11.2 Object Permanence in Animals?

Like the support problem discussed in the main text, many of the cognitive tests for young children devised by Jean Piaget are ideal for comparative studies because they rely on simple nonverbal behaviors. One of the most widely used with animals is object permanence (Dore and Dumas 1987; Gomez 2005). When a very young infant sees an attractive object disappear behind a barrier, she does not search for it. "Out of sight is out of mind." An older infant searches for an object that disappears behind one barrier (A), but if it is moved to a second hiding place (B) while the infant watches, it will be searched for in the first (the "A not B error"). Eventually, around two years of age, children search for objects that are displaced invisibly, for instance while carried in a container. Such behavior is taken as evidence for a concept of object permanence, a simple component of physical cognition, namely, the knowledge that an object still exists when out of sight and the ability to represent its unseen trajectory.

Object permanence develops through six stages, and not all species attain the sixth one (Dore and Dumas 1987; Gomez 2005). Clearly, however, animals could search for disappearing objects without representing their continued existence. The sight of an object disappearing behind an occluder could elicit search behaviors prefunctionally or an animal might learn what to do to retrieve it. For instance, when young domestic chicks watched a mealworm being pulled through a tube and disappearing behind a screen, they did not immediately follow it, but they eventually learned by trial and error to find the hidden worm (Etienne 1973; but see Regolin, Vallortigara, and Zanforlin 1995). As in tests of other abstract concepts, immediate accurate performance in a novel situation is necessary to rule out stimulus generalization of previously reinforced behaviors (Dore and Dumas 1987). Here this means animals that have reached a given stage of object permanence should display evidence of it with novel objects and occluders. In addition, because details such as the relative positions of the hiding places or their configuration can improve or interfere with performance (e.g., Call 2001; Collier-Baker and Suddendorf 2006), conclusions about a species' competence should be based on multiple tests.

Of course there are many natural situations in which animals search for hidden objects. Predators continue tracking prey that have gone into cover; nutcrackers dig up seeds they have buried. Such behaviors may not reveal what animals believe about disappearing objects so much as how well they remember an object's last location (e.g., Dore et al. 1996). But passing an invisible displacement test also seems to imply reasoning: "It's not in the container so it must be behind the screen." Watson and colleagues (2001) used the setup diagrammed in Figure B11.2 to test whether dogs use reasoning or an associative rule to find an invisibly displaced object. Both dogs and 4- to 6-year-old children first saw visible displacements: the experimenter showed a treat in a cup, then walked behind the three screens, stopping at each one to conspicuously either leave the treat or hold it up and replace it in the cup. Nearly all the subjects understood the task right away in that they searched for the treat only when the cup was empty at the end of the experimenter's excursion, although the children were more likely to visit the correct screen first. Then subjects had an invisible displacement test, in which the experimenter moved behind all three screens without showing the treat and then displayed the empty cup. Both children and dogs proceeded to search the three screens in order (the treat was actually not behind any). Consistent with reasoning that if the treat was not behind the first or second screen it must be behind the third, the children speeded up as they searched. In contrast, the dogs slowed down, consistent with some extinction of the previously reinforced searching. The conclusion that they were using an associative rule is supported by evidence from other studies with dogs (Collier-Baker, Davis, and Suddendorf 2004).

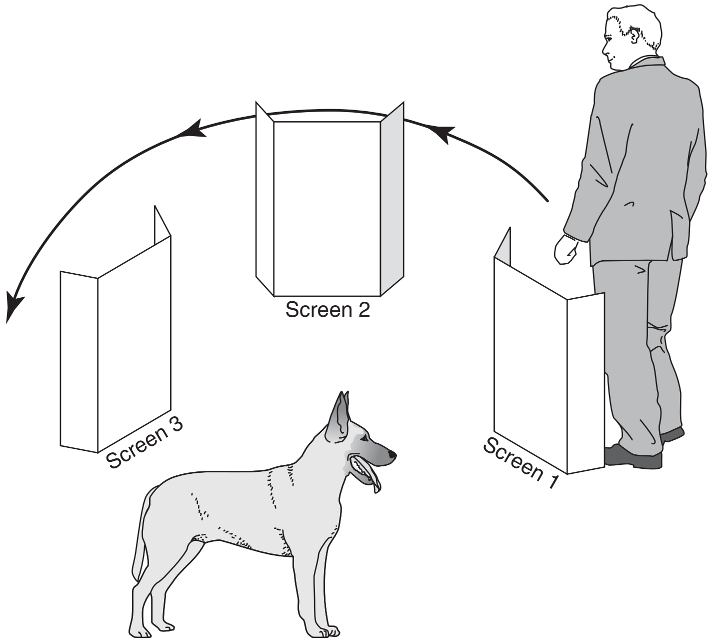


Figure B11.2. Setup used to test dogs and children for their understanding of invisible displacement. In the actual experiment a second person restrained the subject until the experimenter had completed the circuit of the screens and returned to the start area. Adapted from Watson et al. (2001) with permission.

Perception of surrounding or containment is also important for discriminating between effective and ineffective hook tools or canes (Figure 11.20), a test used with chimpanzees (Povinelli 2000) and five species of monkeys and lemurs (Hauser and Santos 2007), as well as with young children (Povinelli 2000; Cox and Smithsman 2006). Interestingly, once animals learn to use a cane of a particular color, thickness, and material, they transfer readily to other tools with the same functional properties even if different in color and texture. For example, tamarins trained with thin blue canes choose a novel thin red cane over an ineffective blue cane (Hauser 1997). Using an object as a tool may focus attention on its functionally relevant features and/or tool-users may be predisposed to attend to such features.

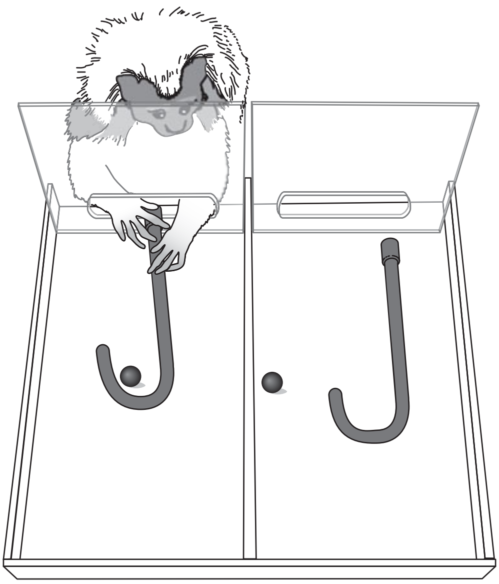


Figure 11.20. A cotton-topped tamarin choosing a hook tool (cane) that surrounds the desired treat over an ineffective tool. After a photograph in Hauser and Santos (2007) with permission.

Normally a tool must be placed in the correct relationship with the goal object, so one might wonder whether tool-using species are better at bringing this relationship about, a skill that seems to require planning a sequence of motor acts (Cox and Smithsman 2006). This issue was addressed by testing capuchins with canes and related tools in a similar way to Hauser's (1997) tamarins (Cummins-Sebree and Fragaszy 2005). Like the tamarins, the capuchins seemed indifferent to the sheer familiarity of a tool's irrelevant features such as color and attended to its functional properties. But unlike the tamarins, which do not use tools in the wild, the capuchins sometimes chose a tool that had not been prepositioned around the food and moved it into position. Their success with such tools improved with practice. These findings are consistent with the capuchins having some sort of specialization for tool-using, perhaps not so much a perceptual or conceptual one as a tendency to engage in certain kinds of exploratory behavior (Cummins-Sebree and Fragaszy 2005). However, as the authors of this study recognized, more thorough comparative work is needed to control for possible differences in, for example, the animals' past experience and their sizes relative to the tools.

Concluding remarks

Shape, size, and orientation do not exhaust the functionally relevant features of tools. Sensitivity to a tool's material has been examined by offering a choice between a floppy and a rigid pulling tool (Povinelli 2000; Santos et al. 2006). But unlike continuity or containment, rigidity cannot be perceived before the tool is chosen. The animal has to recall past experiences with the material, and this requirement may account for failures in such tests. Indeed, it is a mystery why the vervets and tamarins tested by Santos and colleagues (2006) generally rejected a flimsy rope for pulling in food unless some aspect of their past experience predisposed them against it.

Information about what materials animals choose for making tools and how they make those tools also potentially sheds light on the features they regard as important, though again such information cannot be interpreted without knowing the animals' past history, For example, videos of wild chimpanzees arriving at termite nests carrying stout sticks for excavating and/or thin wands for extracting termites as the case requires (Sanz, Morgan, and Gulick 2004) are wonderfully compelling evidence for flexible use of multiple tools and possibly even planning, but tell us nothing about how the behavior develops.

11.4.3 How does tool use develop?

A provisional conclusion from the foregoing section is that using tools involves perceptual and motor skills which tool using species may be predisposed for, but there is no evidence that it involves understanding the unseen causes by which tools work. In this section we look briefly at the development of tool using, in part to see whether this information sheds any new light on what tool users know. Three kinds of learning have been proposed to contribute to the acquisition of tool use: instrumental learning, imitation or some other form of social learning, and insight. Of course insight implies suddenly arriving at understanding without apparent prior practice so solid evidence for it might be thought to settle the question of understanding. However, even if—as does seem to be the case—either or both of the other two mechanisms plays the major role in the development of skilled tool use, this does not rule out the possibility that animals acquire some physical understanding once they begin engaging with tools (Bluff et al. 2007).

Instrumental learning must play some role in the development of skilled tool use—it would be surprising if it did not. Animals should acquire the ways of choosing and manipulating tools that give reward the fastest and most efficiently. An example from the laboratory is the observation that capuchins improved over sessions in placing a hook tool to rake in food (Cummins-Sebree and Fragaszy 2005). But reinforcement works on species-specific predispositions to pick up potential tools like sticks and engage in other behaviors that seem to be precursors of tool use (Schiller 1957; Tebbich et al. 2001; Bluff et al. 2007). This has been best documented in captive young woodpecker finches and New Caledonian crows. They do not need to see adults using tools to start using tools themselves, although social influence may have a role in attracting crows' attention to particular kinds of tools. New Caledonian crows make tools by biting strips off stiff *Pandanus* leaves, and naive socially isolated birds show the rudiments of this behavior. However, the presence of differently shaped tools in different parts of New Caledonia suggests that social learning plays a role in tool manufacture (see Bluff et al. 2007), a possibility we return to in Chapter 13.

The role of social factors in the development of tool manufacture and use by apes and other primates is more difficult to disentangle because of their protracted development and the impossibility of ethically raising them in social isolation. Social learning and the possibility that population-specific forms of tool using in apes are "cultural," that is, socially transmitted, are discussed in Chapter 13. Many of the experiments on imitation and other forms of social learning in apes and monkeys have involved tool-using tasks. As we learn there, true imitation—copying an act from seeing it done—is rare in any species, but numerous other forms of social influence can help to get tool using started, after which the physical requirements of the situation can shape the behavior through individual learning.

Insight

"Aha, I've got it!" In people, this experience accompanies insight, sudden solution of a problem without apparent previous trial and error. The most famous cases of apparent insight in another species were described by Wolfgang Köhler (1959) in the chimpanzees he studied on the island of Tenerife during World War I. They used sticks, strings, and boxes in novel ways to obtain food placed out of reach. For instance, two sticks were joined together to rake bananas into the cage; a box was moved across the cage and used to reach fruit suspended high on the wall. When first confronted with such a problem, animals would usually try the direct solution, jumping up and down under a suspended banana or fruitlessly reaching arms and legs between cage bars. These attempts might be abandoned and the animal might start doing something else when suddenly it would jump up, grab the necessary tool, and immediately solve the problem, as if having experienced an insight into what was required.

Subsequent researchers have emphasized that "insightful" behavior does not appear immediately but may follow many ridiculously (from a human viewpoint) incompetent failures (Povinelli 2000; Machado and Silva 2003). Moreover, experience builds it from species-typical motor patterns (Schiller 1957; review in Beck 1980). Chimpanzees spontaneously carry and climb on boxes, pull strings, play with sticks and put two sticks together. Such experience contributes to solving problems like Köhler's, as does perceptual and motor maturation. Similarly, observations of birds pulling up a dangling string with food on the end reveal a central role for species-typical feeding motor patterns (Vince 1961).

Some insight into precisely how experience with the elements of a solution contributes to "insightful" behavior is provided by a not entirely tongue-in-cheek demonstration that pigeons can solve the banana-and-box problem (Epstein et al. 1984; see also Nakajima and Sato 1993). The pigeons were first trained in two separate parts of the problem. In some sessions they were reinforced with grain for climbing onto a small stationary box and pecking a facsimile of a banana, wherever it was in the testing chamber. Jumping toward the banana was extinguished. In separate interleaved sessions the birds were trained to push the box toward a spot on the wall of the same chamber, with spot and box in varying initial locations. Control birds were trained to climb and peck the banana but did not learn to push the box toward a target. In the critical session, the banana was placed out of reach and the box was available in the chamber, but no spot was present. The birds trained to push directionally all behaved like Köhler's chimpanzees: at first they stretched beneath the banana and looked back and forth between banana and box, but within a minute or so they began to push the box into place under the banana. When the box was in place they climbed onto it and pecked the banana (Figure 11.21).

Films of the pigeons reportedly gave viewers a strong impression of humanlike thoughts and emotions (Epstein. et al. 1984), but a step-by-step analysis of the contingencies involved shows that the behavior can be explained otherwise. Looking back and forth between banana and box at first resulted from their eliciting conflicting responses (Epstein 1985). But because flying and jumping at the banana had already been extinguished, pushing the box quickly became the dominant response. Because both banana and spot had been associated with grain, mediated

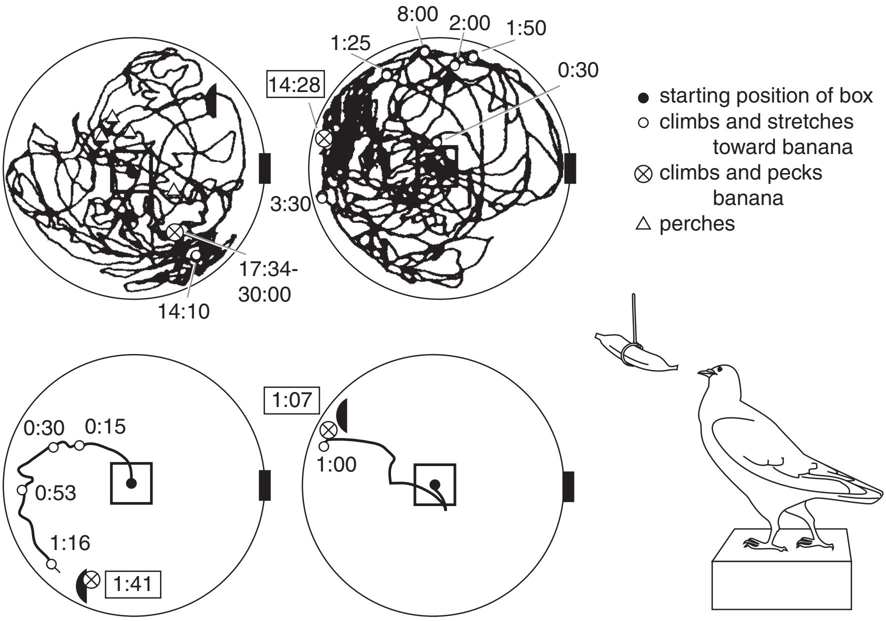


Figure 11.21. Movement of the box during the first 30 minutes of the test of insight in pigeons. Top row: data from two birds trained to push the box, but in no particular direction; bottom row: data from two birds trained to push the box toward a spot on the wall, which was absent in this test. The arena was 69 centimeters in diameter. Times are minutes and seconds from the beginning of the test; time in a rectangle is the time to solution. Redrawn from Epstein et al. (1984) with permission.

generalization (Chapter 6) could account for the banana becoming the target of pushing when the spot was absent. Finally, the birds climbed onto the box when it was under the banana thanks to what Epstein and colleagues call *automatic chaining*. By chance, pushing the box had reinstated a situation (banana within reach) supporting the previously reinforced pecking response. Whether the comparable behavior of Köhler's chimpanzees can be accounted for in a similar way is impossible to say, since their histories were not as thoroughly known.

Epstein and colleagues' account of the pigeons' behavior shows how knowledge of animals' past history and a careful analysis of the stimuli present and the responses they elicit can account for apparently novel or insightful behavior. One mechanism that may have played a role, *resurgence,* has subsequently been well documented (Lieving and Lattal 2003; Reed and Morgan 2007). Resurgence refers to the observation that when two responses are trained in sequence such that the first is extinguished before or during training of the second, the first response reappears during extinction of the second. It is not as well recognized as a source of flexible behavior as it deserves to be. Awareness of resurgence and automatic chaining together with a dispassionate description of actual behavior might take some of the mystery out of other examples of apparently purposeful tool manufacture or use, including examples of using a tool to get another tool ("metatools" Mulcahy, Call, and Dunbar 2005; Taylor et al. 2007).

One much-cited case is the observation that Betty the New Caledonian crow bent a straight wire into a hook and used it as a tool to pull a miniature bucket of meat out of a little well (Weir, Chappell, and Kacelnik 2002). The first time she did this, Betty had already used hooked wires on the bucket, but she was left with only a straight one, and she initially tried to use it. Having failed, she eventually thrust the wire at the base of the transparent well, wedging it in in such a way that it bent when she pulled on it. Now it apparently looked sufficiently similar to hooks she had used in the past to serve as a stimulus for lowering into the well, a successful response for getting the food. Betty was subsequently provided with straight wire on a number of occasions, on most of which she made some sort of bend and got the food, but generally not before trying with the straight wire. However, as Weir, Chappell, and Kacelnik (2002; see also Bluff et al. 2007) acknowledge, only the first trial is relevant as possible evidence of insight or purposeful tool manufacture. Subsequent bends can all be accounted for by reinforcement history. Clearly more subjects are needed, both here and in a further test (Weir and Kacelnik 2006) in which Betty made effective tools by bending and unbending strips of aluminum.

11.4.4 Tool use and causal understanding: Conclusions

Although it has been widely recognized for nearly half a century that making and using tools is not a uniquely human activity, research on nonhuman animal tool use has not yet completely broken free of the snares of anthropomorphism (Wynne 2007a, b). The area lacks a well-developed theory of the abilities required to recognize, use and/or make tools, leaving researchers struggling to grasp what animals understand when they use tools (as in Bluff et al. 2007). In terms of the topic of this chapter, there is no good evidence that anything other than mechanisms of associative instrumental learning discussed in Section 11.3 underlies tool using by any nonhuman species. The role of understanding in humans can be questioned, too (Silva and Silva 2006; but see Penn and Povinelli 2007a). As discussed at length by Povinelli and various colleagues (e.g., Povinelli 2000; Vonk and Povinelli 2006; Penn and Povinelli 2007a), interpreting the world in terms of unseen causes maybe uniquely human. But that is not to say that tool use involves no cognitive specializations. As we have seen, some animals seem quite good at recognizing the functionally relevant features of tools, and this could reflect a predisposition to perceive the affordances of certain classes of objects, if not a preexisting category of tools as a kind of object distinct from foods, landmarks, and other things (Hauser and Santos 2007). Currently the study of animal tool using includes a rich mix of wild and captive animals, natural and contrived tests, birds and primates, species that do and do not naturally use tools. More well-controlled comparative studies could address the question of possible perceptual and representational specializations in tool-using species as well as possible convergence between birds and primates. An example is the parallel studies of apes and corvids by Helme and colleagues (Helme et al. 2006; Helme, Clayton, and Emery 2006). And as in the study of numerical cognition, progress might be made by better contact with theory and data from child development and an attempt to break tool use down into components that may be shared among species to different degrees.

Finally, even though making, using, and culturally transmitting information about tools may be a key component of human civilization, much tool use may not require all that much cognitive complexity. Even people probably learn to use most everyday tools by copying others initially and then perfecting their technique through trial and error. Any folk physics involved is mostly implicit and likely developed though experience with complexes of related tools and tasks—using or seeing others use a hammer, a stone, the heel of a shoe to drive a nail, secure a tent peg, crack a nut, and so on. Poking a stick into a hole and getting out a grub or a candy may not require any more or different understanding than pressing a lever for a food pellet.

11.5 On causal learning and killjoy explanations

In an influential article on cognitive ethology discussed further in the next chapter, the philosopher Daniel Dennett (1983) referred to low-level reflexive accounts of animal deceptive or communicative behavior as "killjoy, bottom of the barrel" explanations. For example, a monkey's alarm call might seem to express an intention to let other monkeys know there is a predator nearby, but maybe it's simply that the sight of a predator when with other animals elicits alarm calling. In these terms, much of this chapter has been an exercise in developing killjoy explanations for kinds of behavior—maximizing long-term intake, planning for the future, learning instrumentally, and using tools—that from an anthropocentric viewpoint seem to demand more complex kinds of understanding. Described from a less value-laden perspective, we have seen the power of basic mechanisms of learning and choice to produce an enormous range of flexible adaptive behaviors without the sorts of explicit understanding people might express in comparable situations. The mechanism underlying rats' behavior in analogues to causal reasoning is still unclear (Waldmann et al. 2008) and not all would agree that animals have no appreciation of qualitatively different causes (Penn and Povinelli 2007a), but whatever the resolution of these debates, an appreciation of how apparent complexity can arise out of cognitive simplicity should be just as much a cause for joy as any validation of anthropomorphism.

Further reading

Overviews of the central issues in this chapter can be found in the book *Rational Animals?* (Hurley and Nudds 2006), especially the chapter by Kacelnik, and in the review by Penn and Povinelli (2007a). *Foraging* (Stephens, Brown, and Ydenberg 2007) and the authoritative text, *Behavioral Ecology* (Danchin, Giraldeau, and Cezilly 2008) provide overviews of current research on optimal foraging. A thorough review of instrumental learning is that by Dickinson and Balleine (2002). Waldmann, Hagmayer, and Blaisdell (2006) and Gopnik and Schulz (2004) provide brief introductions to causal learning, developed further in Gopnik and Schulz (2007) and Waldmann*et al.* (2008). *Decisions, Uncertainty, and the Brain: The Science of Neuroeconomics* (Glimcher 2003) integrates behavioral economics, optimal foraging, animal and human behavior with neuroscience in a clear and readable introduction. For discussions of future planning and related issues, see W. Roberts (2002), Suddendorf and Corballis (2007, 2008a), and Raby and Clayton (2009). Povinelli's (2000) *Folk Physics for Apes* discusses Köhler's (1959) classic work as well as describing the extensive experiments by the author's own group. Tool using by capuchins in field and lab is reviewed by Visalberghi and Fragaszy (2006).

Part III

Social Cognition

Social cognition encompasses all the processes specific to knowing and acting on information about social companions. This includes knowing other individuals' relationship to oneself (e.g., is he friend or foe, dominant or subordinate to me?) and their relationships to one another (e.g., are those two a mated pair, allies, competitors?) For starlings in an anonymous migrating flock or fish in a school such information is of little or no importance, but for animals that form stable groups in which individuals have differentiated social roles, an ability to predict the behavior of known individuals can smooth social relations, allay conflict, and thereby allow more time for feeding, grooming, and resting. Until recently primates were thought to be the only animals with rich networks of social relationships. This assumption led to the theory that the evolution of exceptional cognitive abilities and large brains went hand in hand with the evolution of sociality. Currently, however, the realization that other mammals as well as some birds form groups with similar characteristics are making discussions of this social theory of intellect much more interesting.

In Chapter 12 we begin examining the premise that sociality demands special cognitive abilities of some kind by looking at what individuals know about their social companions. Other animals differ from food, trees, and other parts of the inanimate world in that they have minds. People often explain or predict what others do by attributing mental processes to them: he was angry at someone, trying to deceive me, and so on. Accordingly, a major question in the study of animal social cognition has been whether other animals do the same thing: do animals have theory of mind? Research addressed to this question occupies a large part of Chapter 12. To what extent, if any, is an understanding of other's minds necessary for explaining cooperative, competitive, and/or deceptive behaviors? Again, recent research has expanded to species other than primates, both mammals and birds.

Animals that live in any kind of group can potentially learn from watching their companions, perhaps even be taught or engage in teaching. Chapter 13 looks at what and how animals learn from others, how imitation works, and the controversial proposal that social learning processes have led to animal cultures. Finally, in Chapter 14, we look at communication, intrinsically a social activity, and touch on the possible implications of what we know about animal communication systems for the evolution of human language.

12
Social Intelligence

In traditional studies of learning, social situations were largely neglected. Individual animals were tested in isolation. The same was true in the experimental study of comparative cognition that developed in the 1970s. In classical ethology, social behaviors such as courtship, mating, and aggression were prominent, but they were analyzed in the same way as interactions with the physical world, as sequences of responses to releasing stimuli, here the appearance, vocalizations, and behaviors (displays) of conspecifics (*social releasers*). But more recently, burgeoning information from long-term field studies of primates and other animals along with the cognitive revolution in psychology, theorizing about the evolution of human sociality, interest in human social cognition, even social cognitive neuroscience (Adolphs 2003) and other developments, have transformed the comparative study of social cognition into one of the most lively, fast-moving, interdisciplinary and sometimes controversial areas discussed in this book.

This chapter begins with the *social intelligence hypothesis,* the proposal that living in primatelike social groups requires exceptional cognitive abilities and is therefore associated with high intelligence. Although it was proposed over 40 years ago (Jolly 1966), arguably even earlier (see Cheney and Seyfarth 2007), it is still being debated (cf. Emery, Clayton, and Frith 2007). With only a few exceptions, we still do not know very much about the nature of social knowledge, how it compares across species, and how it is acquired. Is social knowledge qualitatively different from nonsocial knowledge in any way, or is navigating a large social network simply a matter of acquiring an unusually large amount of information? In any case, other individuals are not only social stimuli but have physical features and may administer physical rewards and punishments so their companions can learn about them through domain general mechanisms. Indeed, earlier chapters have included aspects of socially relevant cognition, for example individual recognition (Chapter 5), social concepts (Chapter 6), and reasoning about dominance relationships (Chapter 10). But if there are specifically social forms of cognition, highly social species might be expected to have them to an exceptional degree. To date there are few well controlled tests of this prediction. A promising way forward is with species other than primates, not only mammals such as hyenas and cetaceans (whales and dolphins) but birds and fish.

For human adults, knowing about other individuals means not only being able to predict their behavior but understanding their states of mind, that is, having *theory of* *mind*. Accordingly, the study of animal social cognition prominently includes tests of the mentalistic underpinnings of social interactions. Do animals, for instance, know that other individuals have beliefs, desires, and intentions? This question is no easier to answer than questions about animal episodic memory (Chapter 7), future planning, or physical understanding (Chapter 11). Section 12.3 lays out a framework for approaching it which is then applied to research on animal theory of mind in Section 12.4. Section 12.5 looks at the evolution of cooperative behavior, asking whether any examples of animal cooperation require specialized cognitive abilities or emotional dispositions. We start, however, with a closer look at the nature of social knowledge.

12.1 The social intelligence hypothesis

As set forth by Jolly (1966) and more influentially by Humphrey (1976), the social intelligence hypothesis (also called the social theory of intellect or the Machiavellian intelligence hypothesis, Byrne and Whiten 1988) proposes that social conditions in primate social groups drove the apparently high general intelligence that monkeys and apes seem to reveal in traditional tests of concept formation, learning set, discrimination reversal, and the like as well as their exceptionally large brains in relation to body size. Characteristic of its time, the original theory assumed that intelligence is general rather than modular. From a contemporary perspective, it might instead be suggested that cognitive adaptations for social life are, or have evolved to be, accessible to problems with nonsocial content (Rozin 1976). In any case, the original version of the social theory of intellect implies that complex social organization and general problem solving ability go together, whereas a modular view (e.g., Gigerenzer 1997) implies that they may be independent. In principle, comparative and phylogenetic data can distinguish among these possibilities. For instance, lemurs have a complex social organization but perform more poorly on tests of physical intelligence than Old World monkeys (Jolly, 1966). Because lemurs are prosimians, closer to ancestral primates than monkeys, this finding is consistent with Jolly's suggestion that social intelligence preceded the evolution of equivalent physical intelligence. But in Chapter 10 we saw evidence consistent with some independence between social and physical intelligence in that some corvids whose excellent spatial memory is consistent with their reliance on stored food are outperformed in socially relevant tasks by less spatially adept species (Balda and Kamil 2006).

An often-proposed alternative to the social theory of intellect might be called the foraging theory of intellect. As an example of how foraging niche might select for high intelligence, consider that tropical forests are a complex mosaic of hundreds of tree species, each with its own schedule of fruit and flower production. Because fruits are typically available for a shorter time than leaves, fruit-eating species may be faced with a harder environmental tracking problem than leaf eaters. In addition, a primate troop of a given size needs a larger home range if they eat fruit than leaves since at any given time there may be less food available in it. The foraging theory of intellect therefore predicts that fruit eaters should show evidence of greater generalized learning ability than leaf eaters. Comparison of howler monkeys (leaf eaters) and spider monkeys (fruit eaters) yields evidence consistent with this hypothesis (Milton 1988), though of course data from two species is hardly conclusive. Comparative data on brain size provide more broadly based evidence that fruit versus leaf eating may be correlated with cognitive differences. In bats, rodents, and primates, fruit-eating species have heavier brains relative to their body weights than their leaf-eating relatives (Barton, Purvis, and Harvey 1995). But it takes a longer gut to digest leaves than fruits, so a difference in brain:body ratios could arise because leaf eaters have relatively big bodies rather than relatively small brains. And type of food could have an indirect effect on brain size in that the young of species that eat things requiring more learning to find or process will remain dependent on their natal social group for longer and thereby have more complex social relationships and/or opportunities for social learning.

The social brain hypothesis

As the preceding brief review suggests, the social theory of intellect has become closely bound up with discussion of correlates for the relatively large brains (more specifically, neocortical areas) of primates (Figure 12.1; overall brain:body weight ratios for some primates can be compared to those for other mammals in Figure 2.11). But although overall brain size may be convenient for comparing species, specific cognitive demands might be most strongly reflected in specific areas of the brain (see Chapter 2; Striedter 2005). We need to know more about whether brain areas involved in learning about the physical versus social environments are the same or not before neuroanatomical comparisons can be strong evidence for or against the social theory of intellect (Healy and Rowe 2007). And in any case, sociality and tracking food availability are only two among a "bewildering" (Healy and Rowe 2007) array of factors that have been proposed as selecting for unusually large brains. For example, on one hypothesis (Barton 2000), much of the enlargement of primate brains is accounted for by visual areas. Unlike other mammals, primates have trichromatic color vision (Box 3.1). Red-green discrimination in particular aids in detecting both ripe fruits and tender young leaves, so although it evidently now also functions in social behavior, as witnessed by the colorful faces and bottoms of many monkeys, color vision may have evolved in the context of foraging. In addition, overall primate brain size can be related to innovation rate, an aspect of physical intelligence (Box 2.2; Lefebvre, Reader, and Sol 2004).

One problem is that except in a few well-studied cases we have only a sketchy idea of what social complexity consists of (Kummer et al. 1997). It is not simply a correlate of group size because not all large groups are socially complex. Animals within a flock

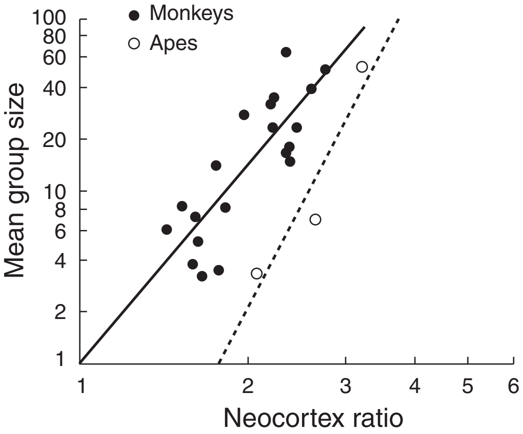


Figure 12.1. Social group size correlated with the ratio of neocortex to the rest of the brain ("neocortex ratio") for monkeys and apes. Each data point is mean for a species. Redrawn from Barrett, Dunbar, and Lycett (2002) with permission.

of birds or a herd of wildebeest may not distinguish among numerous unique individuals and multiple social roles in the way shortly to be described for some primates. However, few if any birds and few nonprimate mammals have been the subjects of the same kind of long-term field studies as some primates. Even within primates, which index is the best proxy for overall social complexity to be correlated with brain measures is disputed. For instance, Figure 12.1 shows a nice relationship between mean overall group size in a species and its ratio of neocortex volume to remaining brain volume, but good correlations have also been shown using other measures such as size of grooming cliques and frequency of deceptive behavior (Dunbar and Shultz 2007). Even worse, this lack of clarity means that attempts to document the social brain hypothesis in other taxa can verge on circularity. Thus the observation (Emery et al. 2007) that larger brains in birds are associated with pair-bonded mating systems, together with the *assumption* that the social brain hypothesis applies to birds, encourages speculation that long-term pair bonds entail special cognitive demands (speculation all too easy to generate from an anthropomorphic perspective). In summary, then, although the social theory of intellect and the associated social brain hypothesis have attracted a lot of attention, thinking in this area is still in flux. The special features of primate brains most likely result from more than one kind of selection pressure (Striedter 2005; Holekamp 2006; Healy and Rowe 2007). Progress will likely come through better information about the roles of different brain areas in social behavior and new statistical techniques allowing multiple factors be considered simultaneously (Dunbar and Shultz 2007) along with more thorough comparisons of social behavior and cognition within groups of related species, both primates and nonprimates.

Why be social anyway?

The species-typical size of animal groups reflects tradeoffs among a multitude of factors related to the nature and distribution of both a species' food and its predators. For example, hamadryas baboons (*Papio hamadryas*) live in the North African semidesert. Food is sparse, and during the day the baboons forage in small bands. However, the safest way for a baboon to sleep is perched on the side of a cliff, and because suitable cliffs are few and far between, as many as 200 baboons gather at night on sleeping cliffs (Kummer 1995). Many birds also congregate to nest or sleep and disperse to forage. In contrast, species dependent on a temporary resource that occurs in large patches, like the grasses of the African plains, forage in large migrating herds or flocks. Still other species are solitary and territorial except for breeding. Other animal social systems were sketched in Chapter 2.

The same costs and benefits determine optimal group size in most species (Section 2.1; Silk 2007a). On the benefit side, an individual foraging in a group can take advantage of others' vigilance and thereby devote more time to feeding (Section 3.7.3). When a predator does attack, the group may be able to confuse it or drive it off. In any case, the effect of the predator on any one individual will be diluted by the presence of others. Individuals foraging together may also help each other find food. They may be attracted to others of their species that are feeding, they may follow each other, as ants follow each other along chemical trails, and they may learn from one another in ways to be described in Chapter 13. But group living may also increase the risk of predation and decrease access to food. For example, a group is more conspicuous to predators than a solitary individual, and animals foraging together may interfere or compete with one another not only for food but also for mates and other resources.

Among some group-living primates, the time-consuming and potentially damaging effects of continual squabbling are minimized by observing a strict social hierarchy that defines priority of access to food and other resources. In addition, comparatively friendly relations are maintained among subgroups comprised of kin or others with alliances of some sort. These relationships are often expressed by animals grooming each other or spending time close together; their extent can be an important predictor of individual fitness (Silk 2007b). Among primates and some other animals, all these social arrangements take place in the context of a comparatively long lifespan and prolonged dependence of the young on their mothers or other adults. Usually members of only one sex, most often males, disperse during adolescence while members of the other stay in their natal area for life. Extended families therefore may contain grandmothers, aunts, cousins, and so on of all ages, the oldest of whom have very extensive knowledge of the local social and physical environment. The slow development that underlies this kind of social group also facilitates growth of a large brain (van Schaik and Deaner 2003; Striedter 2005). Perhaps it is not surprising, then, if large brains and complex societies go together.

12.2 The nature of social knowledge

So far we have taken for granted that living in a social group presents distinctive cognitive problems. But what do animals know about their social companions? Is any aspect of social cognition a distinctive *form* of cognition, as opposed to a distinctive, social, *use* of some more general cognitive ability (Gigerenzer 1997)? Tomasello and Call (1997) concluded from their comprehensive review of primate cognition that primates differ from other animals in being able to learn about *third-party relationships,* a kind of relationship they claimed is uniquely social. As an example, consider dominance relationships. An animal's knowledge about the dominance hierarchy of which it is a part might be entirely in terms of its own, that is, first-party, relationships, perhaps acquired through associating rewards and punishments with particular behaviors directed at particular individuals. For instance, a mid-ranking animal might learn, "If I try to displace Joe from food he moves away and I get the food; if I try to displace Pete, he threatens me." This knowledge implies a third-party relationship, namely Pete is dominant to Joe, which could also be acquired just by watching Pete and Joe interact. As we will see, monkeys are sensitive to many kinds of third-party relationships, but we now know that some nonprimate mammals and some birds and fish are, too.

12.2.1 Social knowledge in primates

Much of what we know about primates' social knowledge comes from long-term field studies, sometimes combined with clever field experiments (see Cheney and Seyfarth 1990; Kummer 1995; Cheney and Seyfarth 2007). A sample from such research illustrates the richness of social relationships to which some primates are sensitive.

Relatedness

We saw in Chapter 6 how Dasser (1988a) used operant category learning to test whether Java monkeys had a concept of the relationship *mother-offspring.* Vervet monkeys tested in the field also show evidence of associating particular infants with their mothers (Cheney and Seyfarth, 1990). When vervets hear the cries of a familiar but temporarily unseen infant broadcast from a concealed speaker, they are more likely to look toward that infant's mother than toward some other monkey. Vervets also show evidence that they are sensitive to more remote kinship relationships among troop members. For instance, a monkey that has recently been the subject of aggression is more likely to behave aggressively toward a relative of its attacker than toward an unrelated monkey. Such *redirected aggression* is seen in many nonprimates as well as primates (Engh et al. 2005). However, while all these observations reveal social knowledge, the processes by which it is acquired need not be specifically social. Mothers and infants are normally seen together and thereby may become associated in the minds of their companions. Relatives may look alike (Vokey. et al. 2004) or become associated through proximity, promoting generalization from one to another. Redirected aggression suggests that the negative effects of fighting with an individual generalize less widely to similar individuals than does the tendency to fight that with animal in the first place.

Male-female relationships

Knowing who belongs with whom or what kind of behavior to expect from A as opposed to B may be explicable as the products of learning mechanisms that are not specific to social stimuli. However, an ability to categorize interactions among specific individuals in terms of kinds of social relationships such as mother-offspring, ally, and so on, that is, to use social concepts, would enable ready generalization to completely new individuals if group membership changes (Seyfarth and Cheney 1994). A pioneer in designing experiments to tap such knowledge was the Swiss ethologist Hans Kummer, working with hamadryas baboons in Ethiopia. In this species, males control "harems" of females. When large numbers of males with their females and offspring gather to sleep and rest, the large powerful males seldom fight over access to females. One male's respect for another's possession of a female arises from observing the two interacting, as Bachmann and Kummer (1980) showed in the experiment depicted in Figure 12.2. The subjects were pairs of males from the same troop and females unfamiliar to them. What would the males do when placed together with a female if *(a)* one had previously seen the other interacting in a friendly manner with the female or *(b)* they had both seen the female before but neither had interacted with her? In the first case, as little as 15 minutes observing the pair inhibited any attempt by the second male to interact with the "married" female and her partner. When introduced into the enclosure with them, he sat in the corner with his back turned and groomed himself or looked at the sky or into the bushes. In the control condition, however, both males tried to interact with the female and occasionally fought over her. These results suggest that the observing male processed what he saw as a particular kind of third-party relationship, one that dictated his staying out of the way of the second male. Quite possibly past experience had taught him to refrain from approaching a female in the presence of a possessing male, but this too requires generalizing over a class of interactions among different individuals.

Further evidence that male baboons rapidly encode information about mating associations comes from more recent work by Crockford and her colleagues (2007) with chacma baboons (*P. cyanocephalus*). In this species, males form temporary consortships with sexually receptive females, during which they stay close to a female and repel mating attempts by rival males. Consortships end abruptly after a few hours

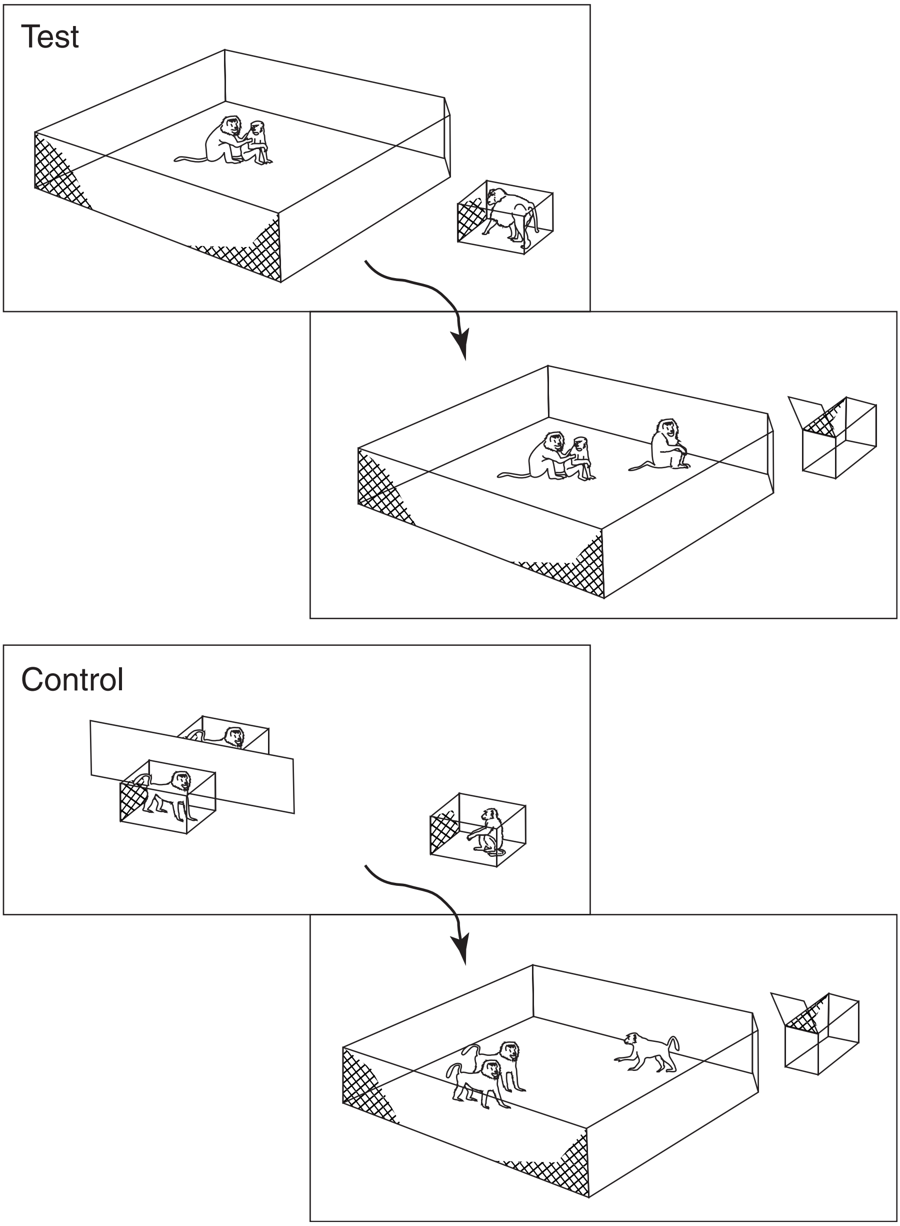


Figure 12.2. Setup and results for a test of male baboons' respect for another male's possession of a female. The Test condition begins with a male watching from the small cage on the right while another male and a female interact. In the Control, first both males see the female in the small cage at the right. Redrawn from Kummer (1995) with permission.

or days while the female is still receptive, opening mating opportunities for others. Males not currently in a consortship were played a recorded copulation call of a female in their group preceded by a grunt from her current or recent consort while both of the consorting animals were well out of sight and earshot. If the consortship was still ongoing and the calls came from the same location or if it had ended and the calls came from different locations, subjects hardly glanced toward the hidden speaker(s). However, if the consortship had been ongoing and the calls came from different locations—as if the consortship had ended—the subject males looked a long time and some even headed toward the speaker from which they had heard the female's call.

Social causation

One might say that the males in the study just described behaved as if performing a kind of causal reasoning: "Those two are have separated because the consortship is over." Another example of such social causal reasoning, this time in chacma baboon females, was provided by Cheney, Seyfarth, and Silk (1995). When a dominant female approaches a subordinate who is holding an infant in an attempt to touch or hold the baby herself, the dominant will often emit a grunt vocalization, and the subordinate may emit a fear bark. If instead a subordinate approaches a dominant, this sequence of vocalizations is never heard. Dominants do not give fear barks to more subordinate individuals. Cheney et al.'s experiment tested whether baboons understand the causal relationship between status of the approaching, grunting, female and fear barking by the female being approached by comparing their reactions to causally consistent and inconsistent sequences of grunts and fear barks (Figure 12.3). In inconsistent sequences, a grunt by a subordinate individual, say F, was followed by the fear bark of a female dominant to her, say C. A consistent sequence matched to this example would also contain F's grunt followed by C's fear bark, but in this case a grunt by an individual dominant to C, say A, preceded C's fear bark. This sequence was causally consistent because C's fear bark could be caused by the approach of A. The consistent sequence contained more vocalizations, so it might

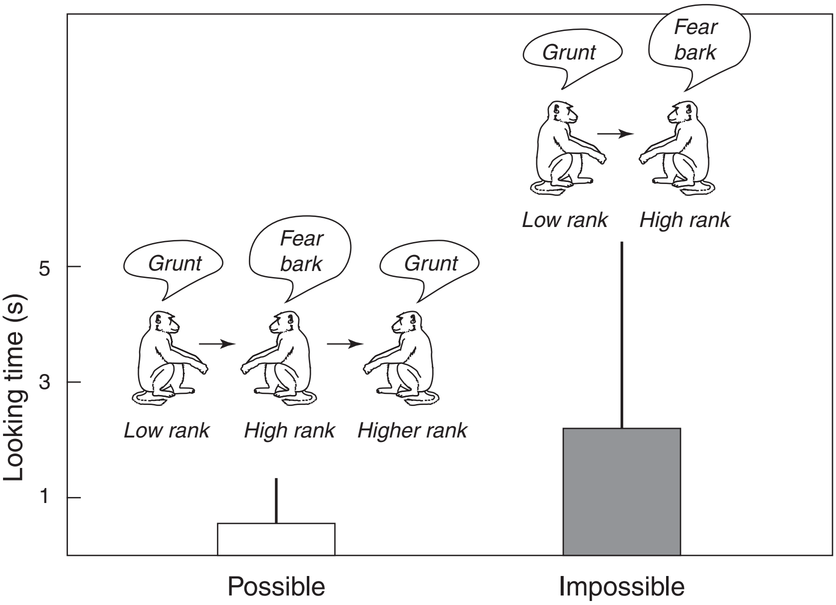


Figure 12.3. Experimental conditions and results of the test of social causal reasoning in baboons. After Hauser (1996) with permission; data from Cheney, Seyfarth, and Silk (1995), redrawn with permission.

be expected to be more salient, and attract more looking, than an inconsistent sequence, the opposite pattern to that expected if the animals are reacting primarily to the information in the sequence.

Each subject heard a consistent sequence on one occasion and an inconsistent sequence on another. On average, subjects looked toward the speaker longer when an inconsistent sequence was played. Because the stimuli were matched for features like the specific vocalizations they contained, these results seem to show that the baboons do recognize a kind of social causation in the sequences of grunts and fear barks. To do so, they need to recognize other individuals' calls and dominance ranks and to know in some sense that fear barks result only from the approach of a dominant toward a less dominant animal. Another possibility, however, is that the specific consistent sequence was simply more familiar. It would be difficult for a study of this kind to escape from such an objection, since it is only through watching and listening to the interactions of other individuals that a subject monkey learns their ranks in the first place.

Alliances and rules of thumb

Monkeys' knowledge about kinship and dominance finds practical expression during agonistic interactions. When two individuals are threatening or fighting each other, bystanders may join relatives or others in *alliances.* Joining may result from *recruitment,* a behavior in which an animal in an agonistic interaction looks back and forth between its opponent and a bystander, the potential recruit. Since rank is power, it makes sense to recruit allies higher ranking than one's opponent. Similarly, a good way to be on the winning side in a fight to join the higher-ranking animal. Both of these choices imply knowledge of third-party relationships, and indeed two species of macaques reveal such knowledge in recruitment and alliances (Silk 1999; Schino, Tiddi, and Di Sorrentino 2006).

Behavior consistent with knowledge of third-party relationships can arise for other reasons (Range and Noë 2005). For example, animals might use rules of thumb like "always recruit the dominant animal" or "always join the winning side" (most likely the more dominant). Relatives may be especially likely to be dragged into each other's disputes simply because they spend a lot of time close together. Unlike in studies with playbacks of social interactions, information about recruitment and alliances is typically extracted from observations of free behavior. Here the only way to control for potential confounds is to start with so much data that subsets of it can be analyzed meaningfully. A good example is the study by Silk (1999) showing that the rank of allies recruited by male bonnet macaques varies with the rank of the opponent (Figure 12.4). We see an example from hyenas in a moment. Still, inevitably a goodly proportion of interactions will be as consistent with rules of thumb as with knowledge of third-party relations (Range and Noë 2005).

Multiple relationships and hierarchies

Taken together, the foregoing information implies that some primates classify their social companions in multiple ways simultaneously, particularly in terms of kinship and dominance, but also in terms of shorter-term relationships like consortship. Evidence for hierarchical classification by family dominance rank and rank within family (Bergman et al. 2003; Schino, Tiddi, and Di Sorrentino 2006) was described in

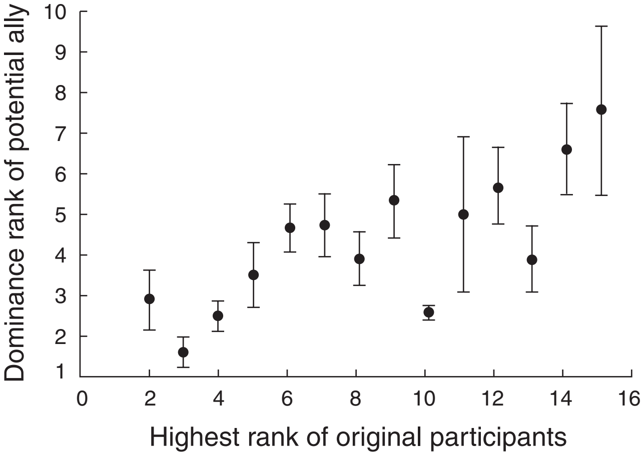


Figure 12.4. Dominance rank of bonnet macaques solicited as allies in an aggressive interaction is higher the higher the rank of the participants. This relationship implies that the animals are sensitive to the relative ranks of third parties, that is, their opponent and potential allies, and not just choosing the highest ranking animal available. After Silk (1999) with permission.

Section 6.5.5 as implying a kind of categorization not yet studied with arbitrary stimuli in the laboratory. As discussed there, learning who belongs to which family has some similarities to learning equivalence classes, but unlike with equivalence classes, the individuals within each class are still differentiated. Seyfarth and Cheney (2003a) have suggested that what is going on is better described as hierarchical chunking of information.

12.2.2 Social knowledge in nonprimates

Elephants, whales, dolphins, and hyenas form long-lasting groups with some of the characteristics of primate societies (see de Waal and Tyack 2003; Bshary and Grutter 2006; Connor 2007). And although it remains to be seen whether any birds or fish form social groups involving such a multiplicity of relationships as those described for primates, some birds and even fish are sensitive to third-party relationships. Not only are studies of social knowledge in such animals fascinating in their own right, but also they provide information that can potentially distinguish among three possible interpretations of the social theory of intellect (Cheney and Seyfarth 2005a). *(1)* Primates exceed all other species in social intelligence. *(2)* Primatelike social cognition is seen in any species with similar numbers and complexity of social relationships. *(3)* Social cognition is similar across species, perhaps because it is qualitatively not different from physical cognition. Accordingly, studies of social cognition in species other than primates are on the increase. This section samples a few that demonstrate knowledge of third-party relationships.

Alliances in hyenas

Spotted hyenas (*Crocuta crocuta*) are carnivores that live in large groups, or clans, similar to primate groups in consisting of individuals from overlapping generations in a network of kin and dominance relationships (Holekamp, Sakai, and Lundrigan

2007). Because carnivores and primates diverged millions of years ago, similarities between them in cognition and brain organization would likely reflect convergent evolution. Like primates, hyenas join conspecifics engaged in agonistic interactions. The knowledge of third-party relationships used in doing so has been analyzed by Engh and colleagues (2005) from extensive records of free behavior just as Silk (1999) has done for monkeys. In the frequent cases where the aggressor was the more dominant of the two original interactants, support by the joining hyena could reflect a rule of thumb ("join the aggressor") rather than knowledge of relative ranks. But in a critical minority of cases a subordinate animal attacked a dominant, and here, too, joiners most often supported the dominant.

Hyenas also show redirected aggression after conflicts. As in primates it is more often directed toward relatives of the former opponent than toward other lower-ranking animals, suggesting that hyenas know about kinship as well as dominance relationships among third parties. These observations may have been biased by relatives of the former opponent being especially likely to be nearby, but they are corroborated by the results of a playback experiment. "Whoops" of hyena cubs not only are recognized by the mothers of the whooping cubs, but they also elicit more looking by the cubs' relatives than by other nearby hyenas (Holekamp et al. 1999). Dominance rank of the cub's mother also influences looking. However, unlike with vervet monkeys, hyenas hearing a cub whooping do not look toward its mother. This could mean they do not recognize the relationship mother-cub, or they may have the requisite knowledge and not express it in looking.

Social transitive inference and eavesdropping and in birds and fish

Some of the best evidence from any species for knowledge of third-party relationships comes from the study of transitive inference in pinyon jays (Paz-y-Mino et al. 2004) discussed in Section 10.3.3. Although the information gained from watching a familiar jay interact with a dominant stranger did not influence more than the first few seconds of the observer's own interaction with the stranger, this is one of the few studies with nonprimate species that rises to the level of Bachmann and Kummer's (1980) experiment with baboons as a well-controlled demonstration that animals can acquire information about third-party relationships by watching. The related study by Grosenick, Clement, and Fernald (2007) provides similar evidence for fish. As discussed in Section 10.3.3, such data suggest that relative information is being encoded as such, perhaps along an analog scale. But the fact that birds and fish learn about the social relationships between pairs of conspecifics was already well established by studies of "eavesdropping" in vocal communication and territorial behavior (see P. McGregor 2005).

The dictionary definition of *eavesdropping* mentions listening in on a secret conversation, but in animal behavior the term refers to extracting any information from the interactions of others, be it auditory, visual, olfactory, or in some other modality (Peake 2005). Importantly—as with *deception, cooperation,* and other terms prominent later in this chapter—this is a functional definition. Deciding whether eavesdropping has occurred does not depend on knowing whether the eavesdropper intended or tried to acquire information, let alone whether it was doing so by stealth, nor does it imply anything about whether the animals eavesdropped upon wanted or intended to provide information. The information acquired by eavesdropping can include absolute features of individuals such as being a good mate or the holder of a certain territory, but some fish and birds also appear to learn about third-party sexual or dominance relationships by eavesdropping.

One example will illustrate the kinds of controls necessary in such studies. Male Siamese fighting fish (*Betta splendens*) are known for showing vigorous aggressive displays as soon as they catch sight of another male. In a study by Oliveira, McGregor, and Latruffe (1998), five males lived in a large tank subdivided as shown in Figure 12.5, with the subject male in the central compartment. After a preliminary exposure to each of his four neighbors, the subject watched (eavesdropped on) a fight between two of them through a one-way glass (i.e., the combatants could not see the eavesdropper). At the same time but unseen by the subject, his two other neighbors had a fight. Following the fights, both of which resulted in a winner and a loser, the

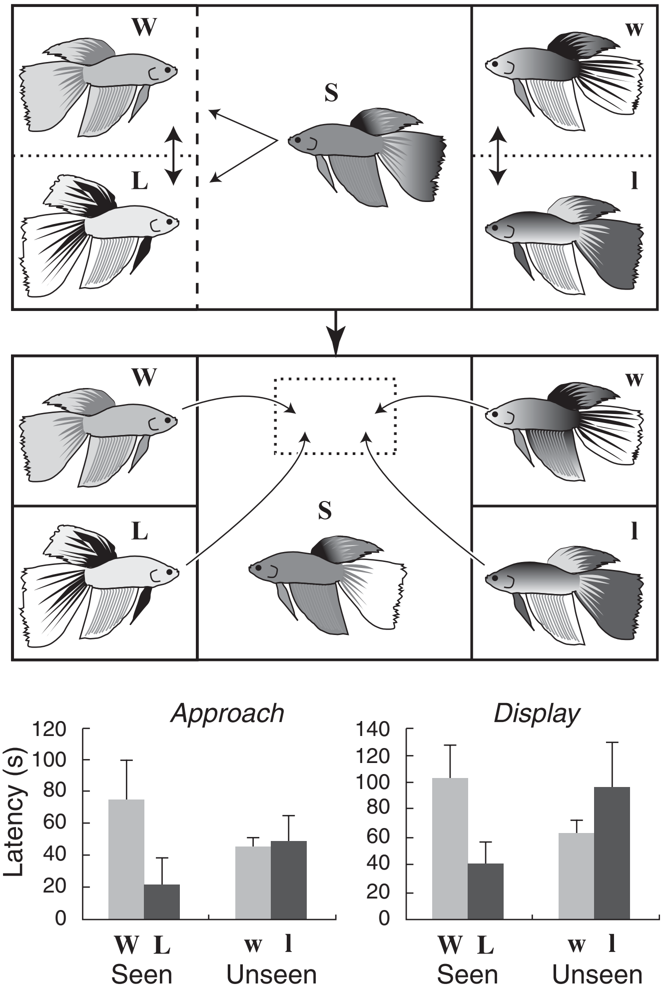


Figure 12.5. Siamese fighting fish learn about third party relationships by eavesdropping. S is the subject; dotted lines = transparent barriers. W, L = winner and loser of fight observed by S; w, 1 = winner and loser of fight not seen by S. Data refer to the behavior of S in the subsequent one-on-one encounters (lower drawing). Adapted from Oliveira, McGregor, and Latruffe (1998) with permission.

subject encountered each of his four neighbors, one at a time in an order balanced across fishes, in a small transparent compartment in his own tank (Figure 12.5). He spent more time displaying toward the winner than the loser of the fight he had witnessed but showed no discrimination between the unseen combatants. The latter data importantly show that discrimination was not based on intrinsic features of the stimulus fish or aftereffects of their having recently won or lost a fight.

Nevertheless, to discriminate between the winner and loser of a fight an observer need not have encoded the relationship between the combatants as such. He may instead encode the level of aggression and/or submission shown by each individual. A followup study by Peake, Matos, and McGregor (2006) supports this account. In their study, male fighting fish again saw two fish engaged in aggressive behavior, but instead of displaying at one another, each of them was displaying at a mirror between their tanks. When one of the "combatants" was made to appear less aggressive than the other by placing the mirror farther from his tank, the observer treated that fish like a loser. In some studies of social eavesdropping in birds, by contrast, researchers have manipulated what a witness is exposed to while keeping constant the total amount of signaling from each interactant. For example, in some species a relationship between two unseen neighbors is expressed in the degree to which a dominant bird's songs overlap those of a submissive neighbor. Studies in which only song overlap is varied have revealed sensitivity to a relationship as such (review in Peake 2005). Similarly, the pinyon jays in Paz-y-Mino and colleagues' (2004) study on social transitive inference saw each bird they were to encounter later both win and lose fights.

Many of the studies of eavesdropping by birds and fish were done with species such as territorial songbirds that typically interact socially with only their mate and a few close neighbors, perhaps only during the breeding season (see Cheney and Seyfarth 2005a). They therefore suggest that knowledge of third-party relationships is not confined to species living in large stable social groups. But the social lives of birds and fish that have larger and perhaps more complex social networks are also beginning to be examined through a primate-centric lens. For example, young rooks in captive flocks form affiliative relationships expressed through behaviors such as mutual preening and food sharing. Rooks also show redirected aggression, and preliminary evidence suggests that it is directed preferentially against the affiliates of an opponent (Emery, Seed, von Bayern, and Clayton. 2007). We look at other aspects of corvid social cognition later in this chapter, but among birds sophisticated social cognition may not be limited to corvids. Graylag geese (*Anser anser*) form long-term family relationships, and families form flocks with clear dominance relationships among families (Scheiber et al. 2005). Among other evidence of such relationships, family members support each other in aggressive interactions. And in fish, one of the most interesting examples of complex social networks is interspecific, in the relationships among cleaner fish and their clients (Section 12.5; Bshary and d'Souza 2005).

Conclusions

In conclusion, the research on social knowledge in nonprimates sampled here seems consistent with the conclusion that primatelike social cognition is not unique to primates. However, primates may still excel in the multiplicity of qualitatively different relationships to which they are sensitive. For example, a female chacma baboon can be at the same time a mother to a particular youngster, a member of a matriline, a member of a within- and a between-family dominance hierarchy, and in a friendship or consortship with a particular male. Some of her relationships are life-long, others are temporary, some are transitive, others intransitive (Cheney and Seyfarth 2005a, 2007). Yet she and the many other baboons in her troop seem to know all these things about one other. The ability of primates to acquire and deploy such knowledge may or may not be the same ability reflected in their performance in tests of abstract concept learning and transitive inference in the laboratory. In any case, it remains to be seen whether long-term, in-depth studies of any nonprimates comparable to those done on a few primate species will reveal comparably sophisticated social knowledge.

12.2.3 Comparing social and nonsocial intelligence

Having sampled the extensive information about what goes on in primate social groups and similar groups of other animals, we can ask whether social knowledge differs in any way from knowledge about the physical world. This question is distinct from that addressed in the next sections of the chapter, namely does social behavior involve social causal understanding such as theory of mind? Here we ask simply, do social situations have a distinctive abstract structure and/or do they engage distinctive learning mechanisms by virtue of their social content?

To see that neither of these questions need have an affirmative answer, think back to the discussion of associative learning and performance rules in Chapter 4 and consider fear conditioning and conditioned taste aversion in rats. Like other examples of associative learning, both are engaged by predictive temporal relationships between events, but the nature of those events determines both the relevant temporal parameters and the behavioral outcomes of experience. Thus, in fear conditioning a close temporal relationship between an exteroceptive signal and shock engages freezing, escaping, and the like, whereas in conditioned taste aversion, experiencing a flavor minutes to hours before gastric distress engages rejection and other disgust responses. One might similarly try to define a social behavior system or module engaged by predictive relationships among particular social stimuli and ask how the conditions for learning compare to those in conditioning. So far only a handful of provocative examples suggests what such an analysis might yield.

Observations of vervet monkeys in the field suggest that they know much less about the physical than the social world (Cheney and Seyfarth 1990). For instance, vervets may have watched as a snake slithering by left a trail on sandy ground, but show no apprehension on encountering a trail in the absence of a snake. Here associative learning expected on the assumption that a fresh trail means a snake is nearby does not seem to occur. Vervets appear to be good social psychologists but poor naturalists (Cheney and Seyfarth 1990). Cheney and Seyfarth (2007) suggest that in addition to possibly learning more quickly about social than nonsocial events, some primates may be predisposed to attend to and learn about dominance and kinship. They support this suggestion with charming accounts of goat-herding baboons that learned spontaneously which kids belonged to each mother goat. But another legendary baboon learned to help a disabled railway signalman by operating switches on the tracks, seemingly more physical than social learning. And as we see in Chapter 14, various animals learn the meaning of the alarm calls of other species, in that they apparently associate calls with the presence of particular predators and behave appropriately.

Returning to social and nonsocial tasks with similar logical structures, recall the comparative studies of transitive inference in scrub jays and pinyon jays from Chapter 10. The highly social pinyon jays learned faster and performed in a more monkey like way on operant transitive inference with colors. This is consistent with the notion that the operant task taps a social cognitive ability, much as operant spatial memory tasks tap the same ability shown in retrieving hoarded seeds (Chapter 8). However, pinyon jays acquire genuine social transitive inference far more quickly than even the first few items in the physical task, suggesting that the tasks tap different abilities. Clearly, however, this comparison is confounded by all sorts of differences between the social and physical tasks. For instance, one involved observing conspecifics; the other, operant conditioning. Even if it were possible to make the conditions for acquisition more similar, equating the salience of the stimuli involved could be an insurmountable challenge. Other jays interacting may grab another jay's attention more than any physical objects. This consideration creates serious obstacles to deciding whether transitive inference, at least in nonhuman animals, is a specifically social cognitive process engaged only weakly by nonsocial stimuli or whether it is a domain-general ability used with any sufficiently salient stimuli.

What it means to compare social and nonsocial reasoning about identical materials is illustrated by studies of the *Wason selection task* with human subjects (see Cosmides and Tooby 1992). As originally studied by the psychologist Peter Wason, this task requires people to look for violations of a logical rule of the form "If p then q." A subject is given the four cards shown in Figure 12.6A and asked which ones need to be turned over to detect violations of the rule, "If a card has *p* on one side it has *q* on the other." Most people turn over the card with *p* on the front to see if it has *q* on the back. Very few turn over only the one necessary additional card, the one with *not q*. Familiar, less abstract, content doesn't always improve performance, but in the example shown in Figure 12.6B, as many as 75% of subjects can detect whether people are drinking illegally by turning over the correct cards.

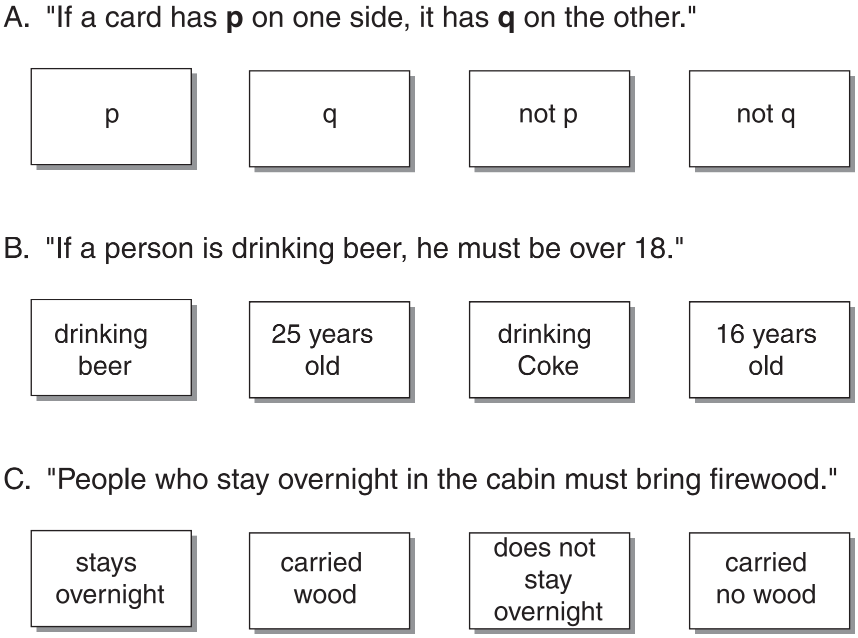


Figure 12.6. Three instantiations of the Wason selection task. After Cosmides (1989) with permission.

According to Cosmides (1989) and others (see J. Evans 2002), the reasoning ability needed here evolved to detect cheaters on social contracts in early hominid society, and the drinking age problem taps into it. Reciprocal altruism depends on participants obeying general rules of the form, "If you take a benefit, you pay a cost." For instance, "If I share my meat with you, you help me gather wood." Cheaters take the benefit without paying the cost, that is, they satisfy the logical condition, "*p* and *not q*." The view that reasoning in the Wason task reflects a cognitive adaptation for social exchange has been supported by the results of experiments in which people are asked to reason about identical statements in a social context versus another sort of context. To control for familiarity of content, Cosmides told Harvard students elaborate stories about fictitious tribes and their customs. Similarly, Gigerenzer and Hug (1992) told subjects stories about people visiting a mountain cabin. When solving the Wason task in these contexts, subjects were much more often correct when "If *p* then *q*"—for instance "People who stay overnight in the cabin must bring firewood" (Figure 12.6C)—was framed as a social contract than when it was framed as a description of social customs.

The approach to human reasoning exemplified by studies of the Wason selection task has been applied to reasoning in other areas, to see whether other examples of apparent irrationality are actually "ecologically rational," that is they make sense when seen as evolved to solve ecologically relevant problems (Todd and Gigerenzer 2007). However, not surprisingly for a task that was already much studied before any evolutionary theorizing about it, the evolutionary psychologists' view that performance on the Wason task reflects adaptations for social transactions is not universally accepted (cf. J. Evans 2002). Nonetheless, like social versus nonsocial transitive inference in the scrub jay, it shows how one might test the idea that similarly structured problems with different content tap qualitatively different cognitive processes.

12.3 Intentionality and social understanding

12.3.1 Levels of intentionality

"I'll pick up the children from school today," says Max as he leaves for work. We'd normally say that Max's statement conveys an intention. We can predict that he will drive from his office to the school by a certain route at a certain time and that he will change his behavior if the circumstances change. If he is working away from the office, he'll travel by a different route and start out at a different time; if the road is blocked, he'll make a detour; if the car breaks down, he'll walk or take a taxi. That is to say, his behavior will be flexible, directed by the goal of being at the school on time.

A philosopher might say that Max exhibits *intentionality,* but she would not mean that Max has intentions in the everyday, folk-psychological, sense. Intention in the philosophical sense is the property of *aboutness* (Dennett 1987; Allen 1995; Dennett 1996). Intentionality, being about things, is perhaps the defining property of mental states. Beliefs and desires, plans, understandings, and wishes, as well as intentions, are examples of *intentional states.* A belief, for instance, has to be a belief about something. A distinguishing feature of intentional statements is that they do not obey the usual logical rules of substitutability. For instance, Max is Susie's father, and Max is a man born in 1950. It follows logically that Susie's father is a man born in 1950. However, Susie can believe that Max is her father without necessarily believing that a man born in 1950 is her father. If we ask whether nonhumans have intentions, beliefs, desires, or the like we are asking whether they are *intentional systems*. Asking this question means formulating clear criteria for what an animal with a certain sort of intentional state does, just as in the tests of belief, desire, and planning discussed in Chapter 11.

Philosophers distinguish a hierarchy of orders of intentionality (Dennett 1983). In terms of this hierarchy, an animal that does not have beliefs, desires, and the like, that is, one that does not in fact have intentional states, is exhibiting zero-order intentionality. Systems of responses to stimuli have zero-order intentionality. A creature that has beliefs, desires, and the like about the real or imagined physical world or the behavior of others is a first-order intentional system. When its mental states concern the mental states of others, we have graduated to second-order intentionality. Thus if Max *plans* to arrive at the school on time, he has first-order intentionality. If he *believes* that the children *know* he is coming for them today, he is exhibiting second-order intentionality. If he *wants* them to *believe* that he *expects* them to be waiting for him, then he is exhibiting third-order intentionality. Level can be piled on level endlessly in this way, but in dealing with animal behavior, it is enough (usually more than enough) to wonder whether one individual is capable of having beliefs or desires regarding another's beliefs and desires (i.e., second-order intentionality), regarding only others' behavior or physical states of the world (first-order intentionality), or neither of those (zero-order intentionality).

In predicting what Max will do when circumstances or his own beliefs and goals change, we are taking *the intentional stance* (Dennett 1983, 1987). That is, we are using the assumption that he is an intentional being to predict and explain his behavior. Most of the time the intentional stance accounts very well for the behavior of other adult human beings. It often provides useful rough and ready predictions of other species' behavior too, but experiments are needed to test them. In Chapter 11 we saw evidence for a first-order intentional account of rats' bar pressing: a hungry rat presses a bar because it both knows pressing leads to food and wants the food. In the arena of social cognition, folk psychology often suggests that animals have second-order intentionality, that is, knowledge or belief about what other individuals know, believe, desire, or intend, but, as illustrated in Box 12.1, a careful ethological analysis may provide a full account of the behavior involved without invoking any form of social cognition as such.

Box 12.1 Intentional Plovers?

When a fox or other predator approaches a nesting piping plover, she doesn't stay and defend her nest but scuttles off, peeping loudly and dragging one wing on the ground as if injured (Figure B12.1). If the fox follows, the bird keeps displaying till she is some way from the nest, upon which she suddenly takes to the air and flies back to her eggs while the fox continues on its way. The broken-wing display thus functions to deceive the fox, but did the plover intend to lead the fox away by pretending to be injured? Or can her behavior be adequately characterized as a system of complex and flexible responses to stimuli typical of predators?

An ethological causal analysis of the broken-wing display would focus on what constitutes "predator" stimuli and the influence of their distance and direction from the nest, the bird's hormonal state, the presence of eggs, and the like. In principle wants, plans, beliefs, or intentions can be causes of behavior, but they were not recognized in classical ethology. Donald Griffin's (e.g., 1978) proposal for a cognitive ethology (see Chapter 1) was a proposal to make room for such causes. As discussed in the main text, one hallmark of intention is that it generates flexible behavior for achieving a goal. Accordingly, one of the

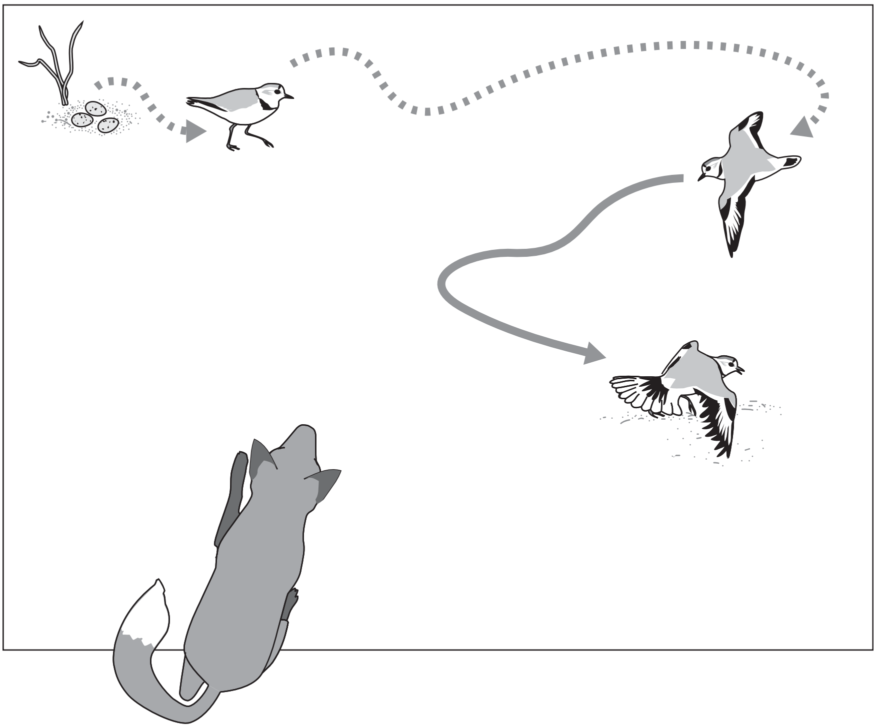


Figure B12.1. Distraction display of a piping plover. From a photograph by Carolyn Ristau.

first studies inspired by Griffin's proposals sought evidence that nesting plovers show flexible behavior toward human intruders consistent with an intention to lead the intruder away (Ristau 1991b). In 87% of staged encounters in which a person approached the nest, the plover did move in a direction that would not take a follower closer to the nest. A "dangerous" intruder also evoked more display than a "nonthreatening" one. If the plover wants to lead the intruder away, it should monitor the intruder's behavior, for instance starting to display when the intruder is facing it. The plover might also be expected to stop when the intruder stops, and perhaps intensify its display or even approach the intruder as if to attract his attention. These predictions also tended to be borne out.

Perhaps because we experience ourselves as acting with specific goals in mind, the control of goal-achieving behavior is the subject of many controversies in animal behavior. But a system can be organized to achieve a given goal without any representation of the goal as such (McFarland 1995; A. Clark 1997). For example, wood lice are found in dark damp places, but they get there because wood lice that are dry and/or in the light move about randomly whereas once they are damp and in the dark they move relatively little (Fraenkel and Gunn 1961). This kind of information implies that we need to ask, what is the nonintentional, classical ethological, alternative to an intentional account of the broken-wing display? As we have seen elsewhere in the book, behavior conditional on combinations of external and internal stimuli can be very flexible. Here it is clearly not the case that the sight of an intruder simply releases a broken wing display in which the bird mindlessly moves in a random direction. The sign stimulus releasing the display seems to include the eyes (Box 12.2) and learned signal value of the intruder. Moreover, the direction in which the bird moves is directed in a sophisticated way by the positions of the bird, the intruder, and the nest, not inconsistent with evidence (Chapter 8) that animals implicitly compute distances and directions and add vectors to locate themselves relative to multiple things in the environment. Clearly an explicit model is needed, a set of if-then statements incorporating assumptions about the stimuli that release and direct the display (Hauser 1996). Taking an approach increasingly practical for testing ideas about behavioral mechanisms and even social cognition (Webb 2000; Dautenhahn 2007) a robot operating according to these rules could be constructed and tested to see if it behaves indistinguishably from a plover. Evidence that it does would imply that the behavior so modeled does not require first-order intentionality, let alone a second-order representation of the predator's knowledge about the nest or its belief in the plover's broken wing.

An example closer to those analyzed later in this chapter is the situation depicted in Figure 12.7: a subordinate male baboon moves behind a rock to solicit sexual contact with a female while out of a dominant male's sight, as if aware that the dominant will not know what he's doing there. The numerous cases of such deceptive behavior in primates described by field workers have been taken as evidence of "Machiavellian intelligence" (Whiten and Byrne 1988). But how can we tell whether the subordinate male's behavior is based on a belief about what the dominant sees or knows? Many animals are sensitive to the direction of other animals' gaze (Box 12.2), as if possessing a low-level perceptual module that detects what other animals are looking at (not the same as the mentalistic "what they are *seeing*"). Our subordinate baboon may well be going behind the rock because he has learned that he escapes punishment for approaching certain females if he is out of the dominant's line of sight; that is, his behavior can be explained as a response to observable cues such as where the dominant is facing. First order intentionality is likely involved: the subordinate *wants* to groom the female undisturbed. But because anything the subordinate might do in response to the dominant's seeing or knowing is inevitably a response to his looking or other behavior, second-order intentionality—the subordinate knows *what the dominant sees* or wants *the dominant to believe* he is just sitting doing nothing—is difficult or impossible to prove. Indeed, as discussed in Section 12.4, Povinelli and his colleagues (Povinelli and Vonk 2004; Penn and Povinelli 2007b) have argued at length that no existing data can distinguish between inference about unobservable

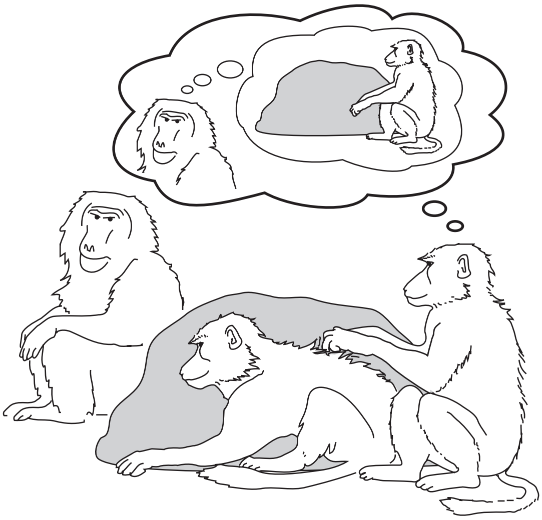


Figure 12.7. Cartoon of the representations implied by imputing intentional deception to a subordinate baboon that conceals its activities from a dominant. Here second order intentionality is depicted: the subordinate, on the right, wants the dominant to believe that there is no other baboon behind the rock. After Byrne (1995) with permission.

mental states of others and inference based on their behavior, facial expressions, and so forth. Although, this argument does not deny second-order intentionality to animals so much as assert the extraordinary difficulty of proving it, the same group (see Chapter 15; Penn, Holyoak, and Povinelli 2008) now claim that no animals possess the requisite representational abilities for theory of mind. In any case, saying that animals respond to each other on the basis of behavioral cues rather than mental states inferred from those cues need not imply that animals treat animate beings as they treat physical objects. Indeed, as we see next, certain kinds of motion trigger perception of animacy and intentionality in human babies, and other primates may also possess such a social perceptual module.

12.3.2 Perceiving animacy and intentionality

Infants' and toddlers' implicit knowledge of physical causality has been tested by showing them a cartoon in which, say, a red ball moves in from the left and collides with a stationary green ball and comparing their looking times to physically impossible versus possible sequels to this event. A possible sequel might be Red stopping and Green moving away to the right, as if Red transferred its momentum to Green. A physically impossible sequel might be Red starting back toward the left with Green close behind it. Even very young infants display considerable implicit knowledge of physical causality in such looking time tests (Spelke and Kinzler 2007). More to the present point, the physically impossible sequence just described would be characterized by adults as a social interaction, Green chases Red (Heider and Simmel 1944). Young children, too, attribute intentional states to very simple inanimate objects moving in certain ways (Scholl and Tremoulet 2000).

Animate objects—most importantly conspecifics, predators, and animal prey—differ from inanimate ones in that they are self-propelled, they can be influenced from a distance without physical contact, and they have goals and intentions. Even infants have expectations specific to self-propelled objects (Scholl and Tremoulet 2000), and this has been taken as evidence for a low-level social module triggered by perception of certain kinds of motion (Gigerenzer 1997). Stimuli for one test of this notion are shown in Figure 12.8. Infants watched a small circle "jump over a barrier" and

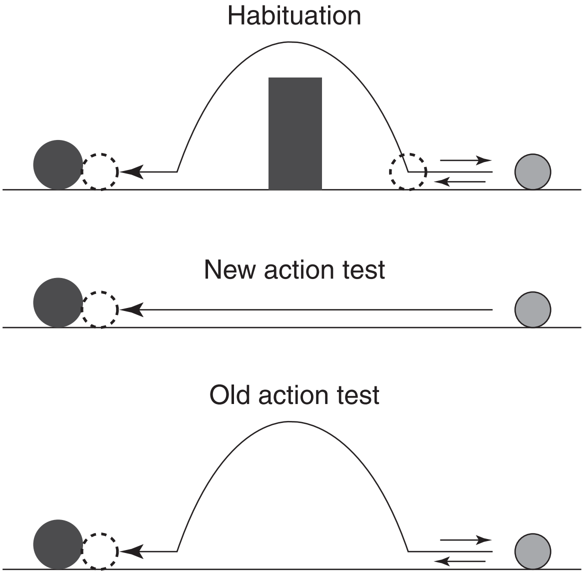


Figure 12.8. Stimuli used to test perception of intentionality in human infants and young chimpanzees. In the habituation phase the small ball moves back and forth briefly then jumps over the barrier. In the test he subject sees one of the lower displays. After Gergely et al. (1995) with permission.

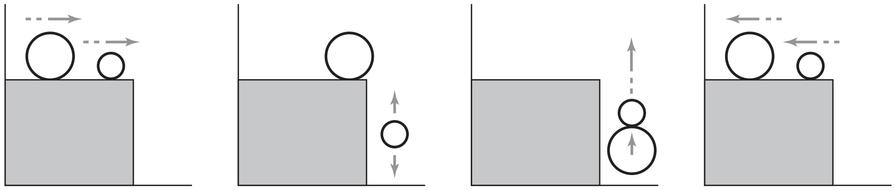


Figure 12.9. Example of a cartoon sequence that would be perceived as depicting intentional, as opposed to purely physical, interactions.

approach a large one. After habituating to this display, they saw one of two test displays in which the barrier no longer separated the two circles. In the old action condition, the small circle still jumped, whereas in the new action condition, it approached the large circle in a straight line. The infants looked longer at the old action than at the new one, but if they had been habituated to the ball jumping without a barrier, this pattern of data was reversed. In effect, they behaved as if representing the moving ball as a rational being approaching a goal and expecting it to take the shortest path available. In one of the few attempts to test for the same kind of encoding in another species, Uller (2004) found similar results in four young chimpanzees.

Not only does self-propelled motion of a lone object trigger a perception of animacy and goal-directedness, displays with more than one such object trigger perception of social interactions (Heider and Simmel 1944; Scholl and Tremoulet 2000; Barrett et al. 2005). Materials from one study with children are sketched in Figure 12.9 (Dasser, Ulbaek, and Premack 1989). In an experimental sequence, the big ball and the small one entered the screen together, the smaller one "fell down the cliff" and bounced around frantically, the big one descended and "helped it up," and they left the screen together. A control sequence consisted of this series of events in reverse order. Children of about three years old looked longer at the experimental than at the control sequence. Furthermore, when the roles of the balls were reversed, children previously shown the experimental sequence looked longer than those previously shown control sequences. Even preverbal infants seem to discriminate between simple shapes (with eyes) that "help" as in the sequence just described, or "hinder." They prefer a "helper" (Hamlin, Wynn, and Bloom 2007).

No tests of primates with similar simplified social stimuli appear to have been reported, but some with pigeons have. Reasoning that interactions between predators and prey should be salient to a vulnerable animal like a pigeon, Goto, Lea, and Dittrich (2002) trained pigeons on a food-rewarded discrimination between displays with four dots moving around at random and displays in which one dot slowly approached one of three others, a display that to people evokes a predator stalking prey. Even after more than 2000 trials, the birds averaged less than 65% correct, suggesting that if pigeons do discriminate intentional from random movement, it is not a salient feature of these displays.

When it comes to perception of intentionality, human gestures have a special status for human babies as young as five or six months (Woodward 1998). In the elegant study of looking times depicted in Figure 12.10, babies saw two toys, here a teddy bear and a ball. The babies were habituated to a hand reaching in from the side and grasping a particular toy. On the test trial the positions of the objects were switched, and the hand reached in again. Now it either grasped the same toy as before, which required a new action, or it performed the old action and grasped the other toy. Babies looked more at the "new object, old action" event, as if they had encoded the

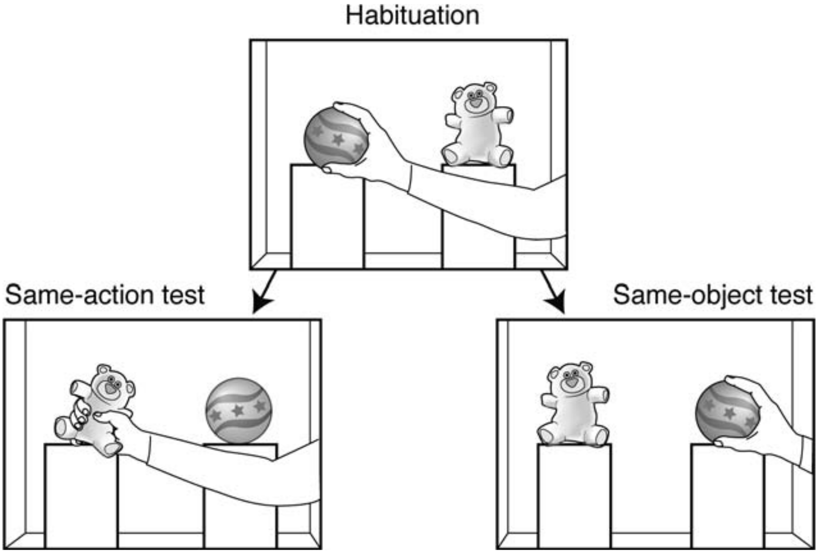


Figure 12.10. Habituation and test events in Woodward's (1998) study of whether infants encode the intentionality of human actions. Redrawn with permission.

action in terms of its goal (grasping a particular toy) and were more surprised to see the goal change than to see a new action performed. This effect did not occur when the hand was replaced by a sponge on a stick or a mechanical claw, suggesting that it is specific to human actions.

In an attempt to see if nonhuman primates behave similarly, a person touched one of two containers or performed an "unintentional" action such as letting their hand flop against it (J. Wood et al. 2007). The animals (cotton-top tamarins, rhesus macaques, and chimpanzees) were then tested to see whether they would look for food in the container that had been touched. Aside from the fact that it is not clear why they would be expected to prefer that container anyway, preferences for the one touched "intentionally" could have been based on past experience seeing people use similar actions to put food into containers (indeed the tamarins tested had been trained extensively to use the intentional action as a cue). In any case, the fact that some animals can apparently predict the outcomes of interactions from a partner's body language and show signs of frustration when the predicted outcome fails to occur does not mean they "understand intentions" in a mentalistic way. The same obviously goes for the infants in similar studies.

In summary, the evidence sketched here shows that animate, potentially socially relevant, objects are discriminated from inanimate ones at a very basic level even by very young infants. The tendency to treat self-propelled objects as goal-directed, a "teleological stance" (Gergely and Csibra 2003), may contribute to the later development of a mentalistic understanding of others' goals and desires but is distinct from it and could be shared with other species. In any case, knowing an individual's goals is distinct from understanding their knowledge or beliefs and from understanding that they have a mental representation of the goal (Perner and Ruffman 2005), but here too, direct perception of simple cues has a role. Individuals of many species acquire knowledge visually, by directing their gaze at things. Accordingly, as shown by a large body of comparative research summarized in Box 12.2,

Box 12.2 Responding to Gaze: Sign Stimulus or Theory of Mind?

The orientation of its head and eyes indicates what visual information an animal is taking in. Accordingly, the eyes of conspecifics or predators can be powerful signals (Coss and Goldthwaite 1995; Emery 2000). For instance, subordinate European jays are more intimidated by a binocular than a monocular glance from a dominant, consistent with the fact that binocular looking is more likely to be followed by attacking (Bossema and Burgler 1980). When rhesus macaque subjects see a video of another rhesus seated between two identical objects looking toward one of them, they appear to attend to the same object (Emery et al. 1997). Sensitivity to a predator's gaze is illustrated by a study in which Hampton (1994) startled captive house sparrows by raising a mask (a model predator) with eyes in different positions or orientations. The birds showed the strongest flight response to a mask with two eyes facing them (Figure B12.2a). The observations described in Box 12.1 suggest that plovers are also sensitive to stimuli correlated with the direction of a potential predator's gaze (see also Watve et al. 2002).

Of greatest interest in this area is *social gaze,* responding to the gaze of conspecifics. Studies described in the main text illustrate how knowing where another individual is looking can be key to success in competitive interactions. In cooperative interactions, too, something worthwhile may usually be learned by following another's gaze. Forward-facing eyes and, in some species, prominent facial markings may make gaze direction a particularly salient social stimulus for diurnal primates (Emery 2000). However, not all species have such conspicuous "whites" of the eyes (sclera) as humans. Thus it is not surprising chimpanzees and some other primates respond primarily to the orientation of the head and/or whole body, even when for practical reasons of experimental control, humans are giving the gaze cues (Emery 2000).

Looking in the same direction as someone else may be an automatic, reflexive, response, rather than evidence of understanding the looker is looking *at* something, that is, of the referential nature of gaze, but the fact that animals also perform effortful responses to get a look at what another individual seems to be gazing at suggests that more is involved. For instance, when chimpanzees are confronted with an experimenter looking at a spot on the wall behind them, they turn around to

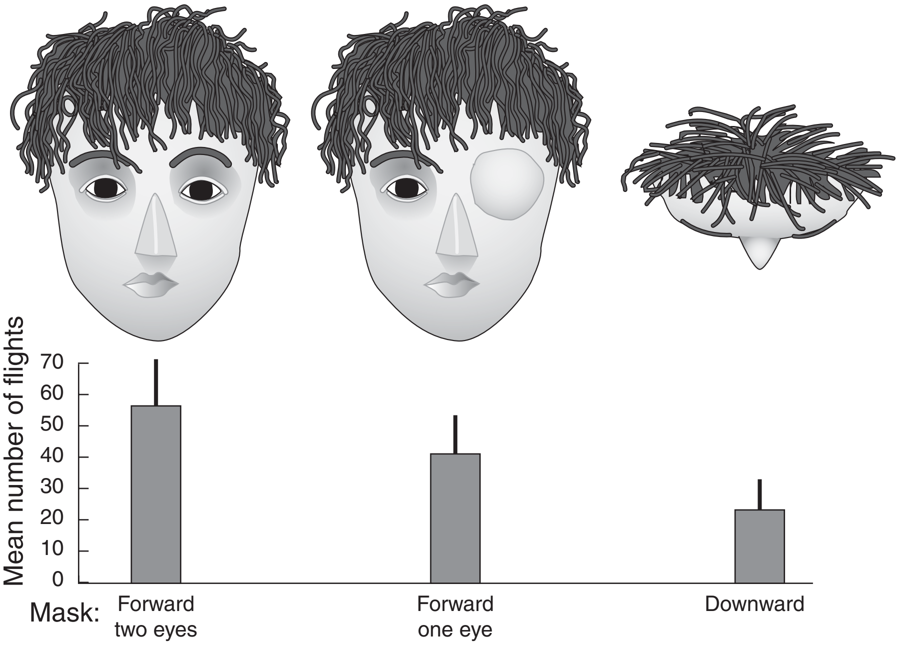


Figure B12.2a. Effect of a simulated predator's direction of gaze (or number of eyes) on escape reactions by captive house sparrows measured as number of flights within an aviary (Hampton 1994). From a photograph by Robert Hampton.

look at it (Figure B12.2b). When confronted with someone looking at a location they cannot see directly, they peer around a partition to get a view of it (Povinelli and Eddy 1996b; Call and Tomasello 2008). Other great apes do the same (Bräuer, Call, and Tomasello 2005). In addition, chimpanzees "check back," that is, alternate looking at the experimenter and the target of his gaze, when they do not see something interesting (reviews in Call and Tomasello 2008; Emery and Clayton 2009). This behavior is also seen in bonobos but to a lesser extent in gorillas and orangutans, consistent with it being an evolutionary precursor of human *shared attention* in which two individuals attend to and communicate about the same thing (Okamoto-Barth, Call, and Tomasello 2007).

Like other behaviors consistent with theory of mind (see main text), some of these more elaborate gaze-following responses are increasingly being documented in birds (Emery 2006) and nonprimate mammals, although they have not yet been analyzed in the same depth (see Okamoto-Barth, Call, and Tomasello 2007). For instance, ravens follow a person's gaze around barriers (Bugnyar, Stöwe, and Heinrich 2004), and goats turn to look in the same direction as another goat (Kaminski et al. 2005). In apes, these behaviors have been taken to support suggestions that the animals "understand seeing," that is, that they have a simple component of theory of mind (Call and Tomasello 2008). This further mentalistic interpretation seems no more demanded here than in the related cases discussed in the main text. Nevertheless, the best answer to the question posed by the heading to this Box is probably "something in between" (Penn and Povinelli in press) in that many animals behave as if knowing that looking normally has a target in ways that seem to go beyond reflexive responses to sign stimuli. Gaze-following is clearly a component of theory of mind, but one precursor to it rather than evidence for it.

Figure B12.2b. A chimpanzee following a person's gaze to the back corner of the cage. The drawing depicts the final stage of a test in which the experimenter begins by facing the chimpanzee and then abruptly switches her gaze. After a photograph in Povinelli (2000) with permission.

animals from birds to apes respond strongly to the direction of another's gaze. Encoding and remembering where others are looking is another basic component of social intelligence that contributes to behavior taken as evidence for theory of mind.

12. 4 Theory of mind

12.4.1 What is theory of mind?

Research on theory of mind stems from a single innovative article (Premack and Woodruff 1978) that inspired a veritable industry of research in developmental and comparative psychology (Carruthers and Smith 1996; Povinelli and Eddy 1996a; Heyes 1998; Wellman, Cross, and Watson 2001; Penn and Povinelli 2007b). As introduced by Premack and Woodruff (1978), having a theory of mind means imputing mental states to others. Theory of mind is evident in intentional deception, using others to gain information by imputing goals, knowledge or belief to them, switching roles, and communicating with intent to inform, among other ways. In the classification of intentional states, theory of mind implies second-order intentionality.

Premack and Woodruff (1978) described a series of tests of whether the chimpanzee Sarah imputed intentions to humans. Sarah, a very special animal with more than 10 years' experience in laboratory tests of cognition, watched short videos in which an actor was thwarted in accomplishing a goal like reaching a banana outside a cage, plugging in a heater, or washing a floor with a hose. The video was stopped and Sarah was allowed to choose between two photographs, one showing the actor about to reach the goal and one not. For instance, the actor might be picking up a long stick to reach the banana or a short one, connecting an intact or a broken hose to a tap. More often than not, Sarah chose the picture showing the action and/or object appropriate to the goal, as if she imputed desires and beliefs to the actor. The fact that she did this in a variety of physically different situations is consistent with behavior arising from a theory of mind. But because she had extensive experience watching people do everyday tasks, she may have been simply choosing the picture that completed a familiar sequence.

Premack and Woodruff sketched several other methods for testing whether a creature's theory of mind extends to imputing knowledge and ignorance to others, but researchers in child development reported the first relevant data (Wimmer and Perner 1983) using what is still (Newton and de Villiers 2007; Penn and Povinelli 2007b) regarded as the acid test of theory of mind, the *false belief test.* Importantly, to pass the false belief test the child must understand that others' beliefs can differ from their own and from the true state of the world. For example, a young child is introduced to a puppet or a person, say a puppet clown. The child and the clown watch as the experimenter hides treat or a toy (Figure 12.11). ("Where is the

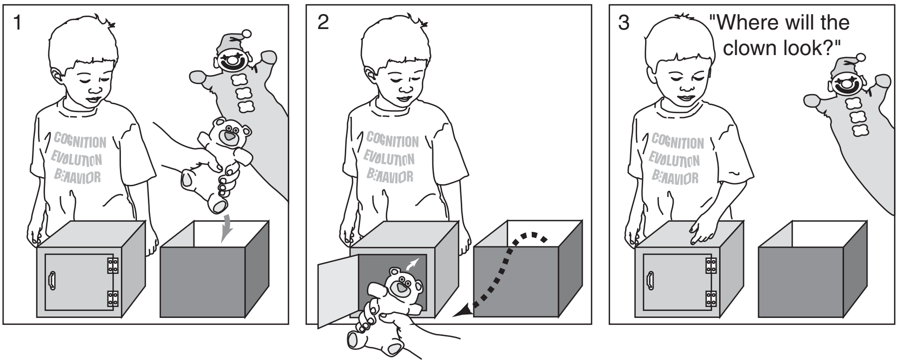


Figure 12.11. A false belief test for three- or four-year-old children.

teddy? . . . In the green box.") Then the clown leaves the scene and the child alone sees the experimenter move the object. ("Now where is the teddy? . . . In the purple box.") Then the clown returns and the child is asked, "Where will he look for the teddy?" Surprisingly, until they are about four years old children predict the ignorant stooge will look where they themselves know the object is ("He will look in the purple box"). They do not seem able to separate their own representation of the situation from another's, or at least they are unable to inhibit the tendency to report on their own knowledge. This finding appears in a variety of situations, and has stimulated much research and theorizing about the young child's theory of mind and how it develops (Wellman, Cross, and Watson 2001; Perner and Ruffman 2005).

12.4.2 Do chimpanzees have theory of mind?

Object choice tasks

One way to test whether, like four-year-olds, nonverbal animals appreciate that seeing leads to knowing is to give them the choice of using information provided by two informants, one of whom has been observed getting access to that information while the other has not (Premack 1988). Thus the subject chooses between two objects as in the false belief task, but the demands of this *object choice task* are simpler because there is no need to keep in mind both one's own and another's beliefs or inhibit reporting on the true state of the world. Povinelli and his colleagues pioneered use of object choice tasks with chimpanzees in an influential series of studies. In the initial experiment (Povinelli, Nelson, and Boysen 1990), there were four food containers, each with a handle that the animal could pull to get the food. As a trial began, the containers were behind a screen, and the animal watched as one experimenter baited a single container in view of a confederate (the Knower), while a second confederate (the Guesser) was out of the room. Then the Guesser returned, and Knower and Guesser each pointed to a container as the chimpanzee was allowed to make a choice. A creature whose theory of mind encompasses the understanding that seeing conveys knowledge would obviously choose the container indicated by the Knower, and in fact, all four chimpanzees tested chose correctly some of the time. However, because the experiment went on for 300 trials, the animals had plenty of opportunity to learn a conditional discrimination: choose the person who was in the room when the container was baited. Consistent with this interpretation, choices of the Knower increased across trials. The study therefore concluded with a novel transfer test in which both Knower and Guesser were in the room when the container was baited, but the Guesser had a paper bag over his head. Over all 30 trials of this test, three of the chimpanzees still chose the Knower. However, they chose randomly on the first two such trials (Povinelli 1994), a result more consistent with the conclusion that they quickly learned to choose the person who had not worn a bag than with knowledge attribution. Importantly, object choice does seem to be a good test of theory of mind development in children: in a similar procedure more four-year-olds than three-year-olds consistently chose the Knower (Povinelli and deBlois 1992).

These negative findings were only the beginning of the quest for theory of mindlike abilities in chimpanzees. The next stage was to simplify the Knower/Guesser paradigm into a more direct test of knowledge attribution that did not require remembering where different individuals were looking. In this test, animals need only appreciate that gazing at something (Box 12.2) means seeing it, that is, having some knowledge about the thing being looked at. This approach was taken by Povinelli and

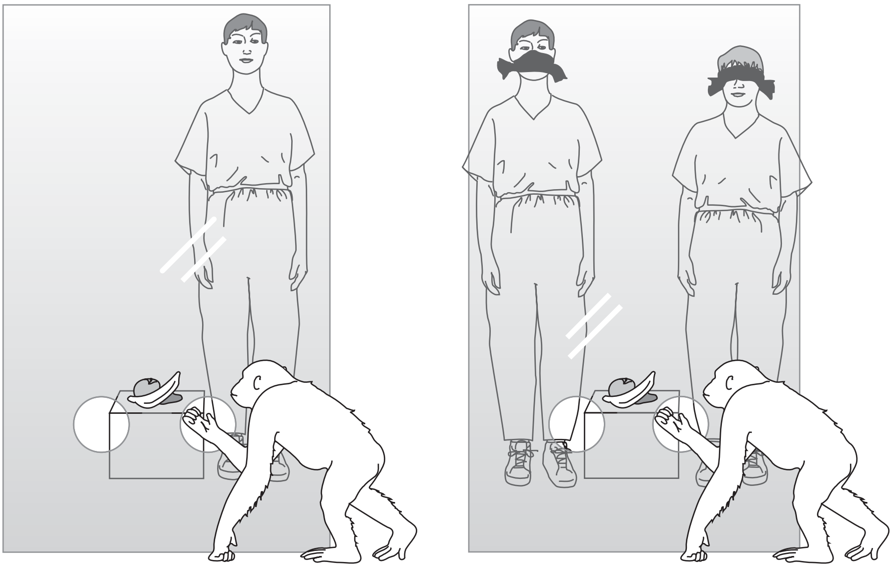


Figure 12.12. Example of Povinelli and Eddy's object choice tests for chimpanzees. Left: control condition. The animal is given the food for directing a begging gesture through the hole in front of the experimenter. Right: the animal will receive food for gesturing toward the experimenter that can see him. After photographs in Povinelli and Preuss (1995) with permission.

Eddy (1996a, 1996b, 1996c) with young chimpanzees. The animals were trained to gesture through a hole in a transparent plexiglas wall toward an experimenter holding food on the other side (Figure 12.12). The wall had two holes, with the experimenter positioned in front of one. The animal received the treat only for reaching through the hole closer to the experimenter. To be sure the animals were attending to what was being offered, occasional probe trials were administered in which one experimenter sat near each hole, one holding a block of wood and the other, a food treat. Both experimenters looked straight ahead, at the plexiglas wall, not attempting to meet the chimpanzee's gaze. Once the animals discriminated very reliably between the two experimenters on probe trials, Povinelli and Eddy started a series of tests in which both experimenters held out food but one could clearly see the chimpanzee as before, whereas the other could not. For instance, the "non-attending" experimenter might be wearing a blindfold, have her hands or a cardboard screen over her eyes, or her back to the chimpanzee. Controls for having something unusual on the face included the "attending" experimenter having a blindfold or hands over her mouth or a cardboard screen beside her face. Such tests were intermixed with normal trials and occasional probes with a block of wood versus food. The chimpanzee was always rewarded for begging from the experimenter who could see.

The surprising result of these experiments was that in nearly every type of test the chimpanzees gestured as often to the experimenter who could not see them as to the experimenter who could. This was despite the fact that the animals performed well in the continuing regular trials and probes with the block of wood. The exception to random behavior was that when one experimenter had his back turned, the chimpanzees tended to choose the experimenter who was facing them. Even this did not indicate an understanding of seeing as attention because when both experimenters turned their backs while one looked over her shoulder toward the subject, choice reverted to random. Over trials of all kinds, however, the proportion of choices of the "attending" experimenter gradually crept above 50%, indicating that the chimpanzees were learning, perhaps to choose the person whose eyes were visible.

Povinelli and Eddy concluded that although their subjects were very good at detecting where someone was looking (Box 12.2), chimpanzees do not understand seeing as attention and/or knowledge but can learn to direct behavior selectively to people who are looking at them. Even on the view that experiments like Povinelli and Eddy's cannot in principle establish more than chimpanzees' sensitivity to behavioral cues, their animals' failure to respond more readily, if not spontaneously, to such cues is surprising in the light of the sophisticated social cognition generally attributed to chimpanzees (e.g., by Byrne and Whiten 1988; Whiten and Byrne 1988). Predictably, then, many reasons were found to challenge their conclusion (e.g., Gomez 1996; P. Smith 1996; Tomasello, Call, and Hare 2003). Two questionable aspects of their procedure turn out to be key. First, the animals in Povinelli and Eddy's experiments were confronted with potentially helpful individuals whereas in nature chimpanzees may more often compete than cooperate over food (but see Penn and Povinelli 2007b). Moreover, because the helpful individuals were humans rather than other chimpanzees, the experiments tested the (captive) chimpanzees' theory of the *human* mind, or at least their ability to take behavioral cues from humans. Hare and colleagues tackled both of these issues in a new series of experiments.

Chimpanzees compete for food

In the setup developed by Hare and colleagues (2000) two chimpanzees, one dominant to the other, are in cages on either side of a central area with one or more barriers or containers where food can be placed. In the study depicted in Figure 12.13, two pieces of food are placed in the central cage while the doors to the side cages are closed. One is visible to both animals whereas the other is visible only to the

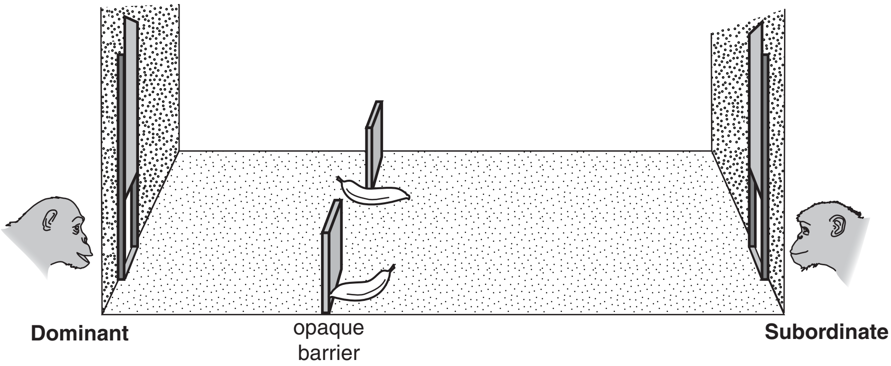


Figure 12.13. Test of whether chimpanzees behave as if knowing what another chimpanzee can see in a competition over food. The animals are shown just before being released into the central arena. The subordinate will get a slight head start; the food is closer to the dominant's end to enhance the competition. Adapted from Bräuer, Call, and Tomasello (2007) with permission.

subordinate because the barrier shields it from the dominant's view. When the doors are open, will the subordinate prefer to head toward the piece of food the dominant cannot look at? This question was answered in the affirmative for several variants of the situation in Figure 12.13 (Hare et al. 2000). The same was not true of capuchin monkeys in a similar test (Hare et al. 2003; see also Burkart and Heschl 2007). With the chimpanzees, various controls ruled out possibilities such as the subordinate preferring to eat near a barrier. However, these effects are not evident in all measures of the subjects' behavior and depend on details of the setup that influence the intensity of competition. For example, if the pieces of food are both closer to the dominant or are so close together that one animal can easily reach both, subordinates show no preference (Karin-D'Arcy and Povinelli 2002; Bräuer, Call, and Tomasello 2007).

Not only may chimpanzees respond as if knowing what another can see in a competitive situation, they may remember what others have looked at, leading them to behave as if knowing what others know (Hare, Call, and Tomasello 2001). Food was hidden in a setup like that depicted in Figure 12.13 while the subordinate animal watched. The critical variable was whether the dominant was also watching, that is, whether it could know where the food was and thus be a strong competitor when both animals were released. Subordinates were more likely to obtain the food when the dominant had not seen it hidden. Moreover, subordinates discriminated between a dominant present during the baiting and one that had not seen it, getting the hidden food more often in the latter case as if knowing what a particular animal knew. They did not, however, discriminate in a more demanding situation that required remembering which of two pieces of food the competitor had seen being hidden.

Chimpanzees' sensitivity to others' behavior in these tests may indeed be favored by the situation being one of competition rather than by the fact that it involves conspecifics instead of humans. This conclusion is supported by the finding (Hare and Tomasello 2004) that subject chimpanzees were somewhat more successful in choosing the correct container in a simple object choice task when a human or a chimpanzee "informant" behaved in a competitive rather than in a cooperative manner toward them. Because some of the reaching and pointing cues used by the humans were similar in the two contexts, these findings suggest that competition enhances either the salience of such cues or chimpanzees' motivation to attend to or use them. Notice that this says nothing about theory of mind but a great deal about predispositions to respond to and/or remember certain kinds of behavioral cues. The importance of such predispositions is underlined by the success of dogs in similar tasks.

Dogs take cues from humans

Pet dogs are very good at locating hidden food when a person points to it or gazes toward it (reviews in Hare and Tomasello 2005; Miklosi 2007; Udell and Wynne 2008; Reid 2009). Indeed, they perform substantially better with a variety of human communicative cues than do apes tested in a comparable way. For example, in one study (Bräuer et al. 2006) dogs chose the container a person pointed to in 90% of trials whereas chimpanzees and bonobos chose it only 60% of the time. Several explanations have been proposed for dogs' skill in such tasks: canids versus primates, domesticated versus nondomesticated species, more versus less experience with human cues (Reid 2009). One prominent early study (Hare et al. 2002) indicated that domestication was key. Puppies from a kennel immediately responded to gazing, pointing and the like, but captive wolves with extensive exposure to humans did not. However, when the testing conditions are more rigorously equated across groups, wolves with exposure to people can outperform pet dogs, and stray dogs from shelters perform very poorly (Udell, Dorey, and Wynne 2008). These findings implicate pet dogs' extensive experience with people, especially with their hands as sources of food (Wynne, Udell, and Lord 2008; Reid 2009). But this does not mean the genetic changes accompanying domestication are unimportant. Domestication of dogs may have involved increasing their usefulness to people by selecting for responsiveness to cues from humans. Alternatively, highest reproductive success may have gone to the animals least fearful and aggressive toward humans, with responsiveness to human behavioral cues as a byproduct. Evidence for this hypothesis comes from the finding that foxes selected for 45 generations for low fear and aggression toward people, but not control foxes, behave like dogs in an object choice task with human cues (Hare and Tomasello 2005). Most likely both domestication and experience are important: selection for attentiveness to human actions may have led to a propensity for rapid early learning about human cues (Reid 2009). Clearly more extensive studies are needed of how dogs' and other canids' responsiveness to humans develops from a very early age. In the meanwhile, the discussion has strayed away from theory of mind into analysis of how animals respond to cues from people. One way back toward theory of mind is to look at natural situations in which animals behave as if knowing what their conspecifics see or know.

12.4.3 Food storing birds remember who was watching

Some socially living food-storing birds are able to remember where they saw their companions caching food (Section 7.4.2). To protect its caches from thieves, a storer in such a group should attend to whether others can see it while it is caching and have strategies for reducing the chances that observers later pilfer its caches. A number of food storing species use such strategies (Dally, Clayton, and Emery 2006; Pravosudov 2008). The cognitive processes involved have begun to be analyzed in two of them, ravens and Western scrub jays. The examples summarized here (for others see Clayton, Dally, and Emery 2007) show that food-storing corvids are very good at detecting and remembering what others have watched. As a result they can equal chimpanzees in behavior consistent with theory of mind.

Figure 12.14 depicts the setup for an experiment in which a captive raven cached meat in a large aviary while two flockmates, both subordinate to it, were in separate cages at the side (Bugnyar and Heinrich 2005). One could see the cacher and thus could potentially pilfer the caches, whereas the other's cage was enclosed by curtains. Five minutes after the caching trial the cacher was returned to the aviary either alone or with the observer or nonobserver. As would be predicted if the cacher remembered which bird observed the caching and treated it as a potential pilferer, subjects retrieved more of their caches in an observer's presence than when alone or with a nonobserver. This effect was evident primarily when the second bird was close to caches. That is, subjects were quick to retrieve caches that a knowledgeable competitor was approaching but, if anything, in the presence of an ignorant competitor they selectively retrieved caches at a distance from the second bird. Observers tested alone did in fact know where the caches were and nonobservers did not, as evidenced by differences in their latencies to pilfer the caches. Latencies of observers and nonobservers did not differ significantly in trials when the cacher was present, mainly because the observer was slower to approach the caches in those conditions. Thus cachers may not have been able to detect observers on the basis of their approach behavior but rather needed to remember that they had been watching. Nonetheless,

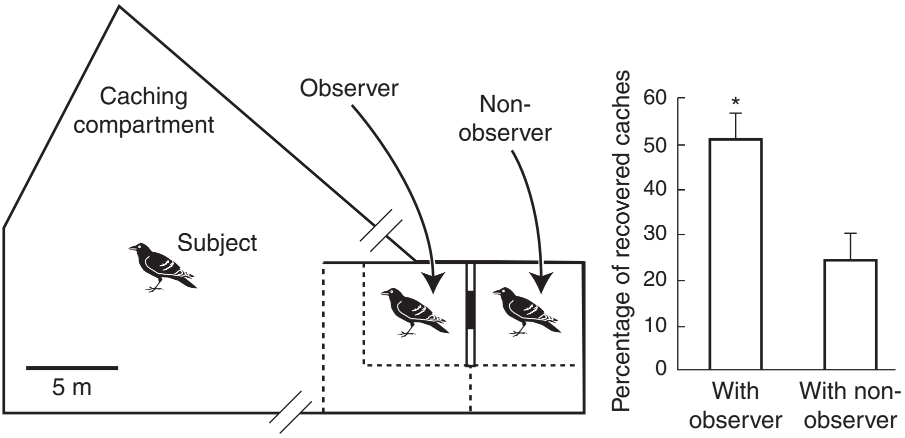


Figure 12.14. Setup for test of whether ravens remember who was watching as they cached. Dotted lines represent transparent barriers. During caching by the subject, the observer and nonobserver were as shown. Data show what happened (as proportion of caches recovered) when the subject was returned to the caching compartment along with the observer or the non observer. After Bugnyar and Heinrich (2005) with permission.

the raven subjects themselves might have been detecting behavioral cues from potential pilferers that were not obvious to people. The same reservation applies to the second experiment in this study, in which the focus was on whether potential pilferers remembered which other ravens had observed caches being made and thus might compete to pilfer them.

In any test of any animal's ability to discriminate between a "knower" and a "guesser," if the roles of knower and guesser are played by animals that do genuinely differ in their knowledge, it is difficult to rule out the possibility that subjects are responding to some subtle differences in those animals' behavior in the test. This problem was tackled by Dally, Emery, and Clayton (2006) in a study with scrub jays that, like Bugnyar and Heinrich's (2005) study with ravens, tested birds' memory for who had witnessed a particular episode of food caching. Here, the birds cached in distinctively marked trays in their home cage. Observers in an adjoining cage never actually competed to retrieve caches but simply watched (or not) at retrieval. The primary measure of whether they were treated as potential competitors was the number of items subjects moved to new locations during retrieval. This recaching behavior is thought to reduce pilfering by observers by overloading or interfering with memory (DallyClayton & Emery, 2006). An earlier study (Emery and Clayton 2001) indicated that scrub jays need experience pilfering the caches of others to show this response to potential pilferers of their own caches, as if projecting their own experience onto others. However, because only small amounts of recaching were shown in this study, and the birds all had extensive past experience in other studies, this provocative finding needs replicating with naive birds pretested for recaching and then assigned randomly to pilfering or control experience.

To return to the study of Dally, Emery, and Clayton (2006), here jays recovering items in private recached more of them when caching had been observed by a dominant bird than by its partner, by a subordinate, or no bird at all. Because these differences occurred in constant conditions, with the subject alone, they are

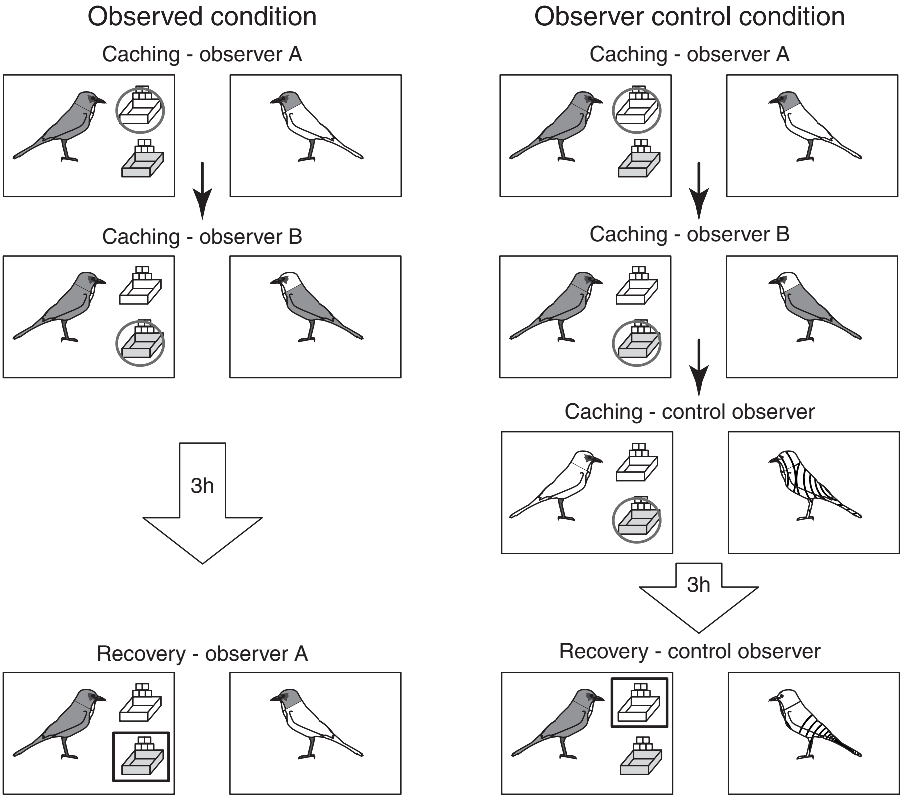


Figure 12.15. The procedure for the experiment with scrub jays by Dally, Clayton, and Emery (2006). Circles around caching trays indicate Plexiglas covers, forcing the subject to cache in just one tray. Square surrounding a tray in the recovery phase indicates the tray in which caching has been observed by the observer present for that test. After Clayton, Dally, and Emery (2007) with permission.

consistent with memory for the type of bird present during caching. To test whether that memory was for a specific individual, in a further experiment jays cached in two different trays, each watched by a different observer, one of which was present while the subject could retrieve from both trays (Figure 12.15). Subjects recached significantly more items from the tray that bird had observed than from the tray observed by a different bird. Of course an observer may have looked in some special way at the tray that it knew had been cached in or otherwise behaved differently toward it than toward the second tray. However, when subjects were watched at recovery by a bird that had seen a *different* subject cache in one of the same trays, recaching was at a low level and did not differ between the trays. These findings indicate that in addition to remembering what, where, and how long ago they cached (Chapter 7), scrub jays remember who was present when they cached in particular places and behave as if aware of other individuals' knowledge. Of course the cacher's behavior could instead have reflected different behaviors by the control and the actual observers, but this difference in itself would mean that scrub jays (in this case observers) know who cached where. In any case, it appears that scrub jays, like ravens and probably other corvids (see Clayton, Dally, and Emery 2007), have detailed social knowledge that they deploy in defending their caches from potential pilferers.

12.4.4 Behavioral abstractions or theory of mind?

The fundamental question about animal theory of mind is whether animals reason about others' mental states or respond to their behavior alone. As Premack and Woodruff (1978) put it, "Is the chimpanzee a behaviorist or a mentalist?" But because inferences about mental states are based on current or remembered behavior it is impossible to be only a mentalist. As we have seen, no existing data demand explanation in terms of theory of mind, but neither do they conclusively rule it out (see also Cheney and Seyfarth 2007; Penn and Povinelli 2007b; Emery and Clayton 2009). Is it even possible in principle to decide whether or not any nonverbal creature has a theory of mind? We look here at three proposed answers to this question, starting with a fresh look at what having a theory of mind entails.

Theory of mind as an intervening variable

We—and perhaps monkeys too—infer that Monkey B wants bananas not only because he looks avidly at Monkey A's banana, but also because he eats bananas whenever possible, he climbs tall trees to get bananas, and so on. The situation parallels that facing motivation theorists deciding, for example, when to describe a rat as thirsty as opposed to merely drinking in response to external stimuli (Whiten 1996). In the traditional language of experimental psychology, a theory of mind or a motivational state is an intervening variable (Sober 1998). The animal as psychologist and the human as animal psychologist have the same problem (Whiten 1994). It becomes defensible to infer such a variable if behavior can be described more economically and predicted more effectively by doing so than by not doing so (Figure 12.16). Thus we cannot tell if Monkey A is imputing desire and belief to B if all we observe is A concealing bananas from B. An animal that has a theory of mind

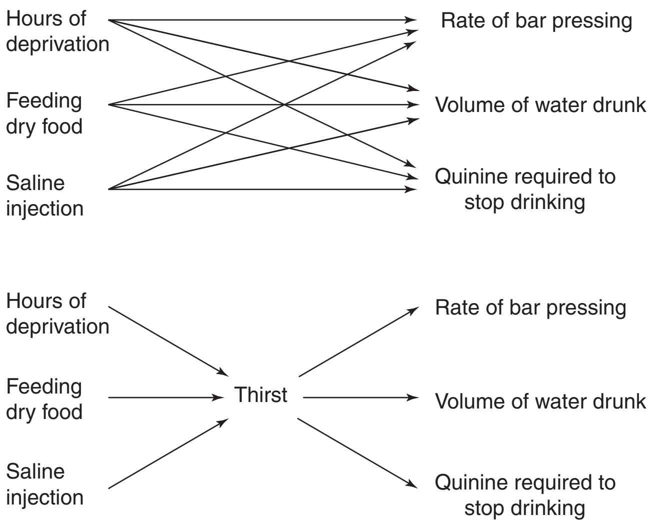


Figure 12.16. *Thirst* as an intervening variable that summarizes efficiently the pairwise relationships between each of three independent variables and three kinds of behavioral observations. If only, say, deprivation and rate of bar pressing had been looked at, the inference of a mediating internal state would complicate rather than simplify matters. Redrawn from N. Miller (1959) with permission.

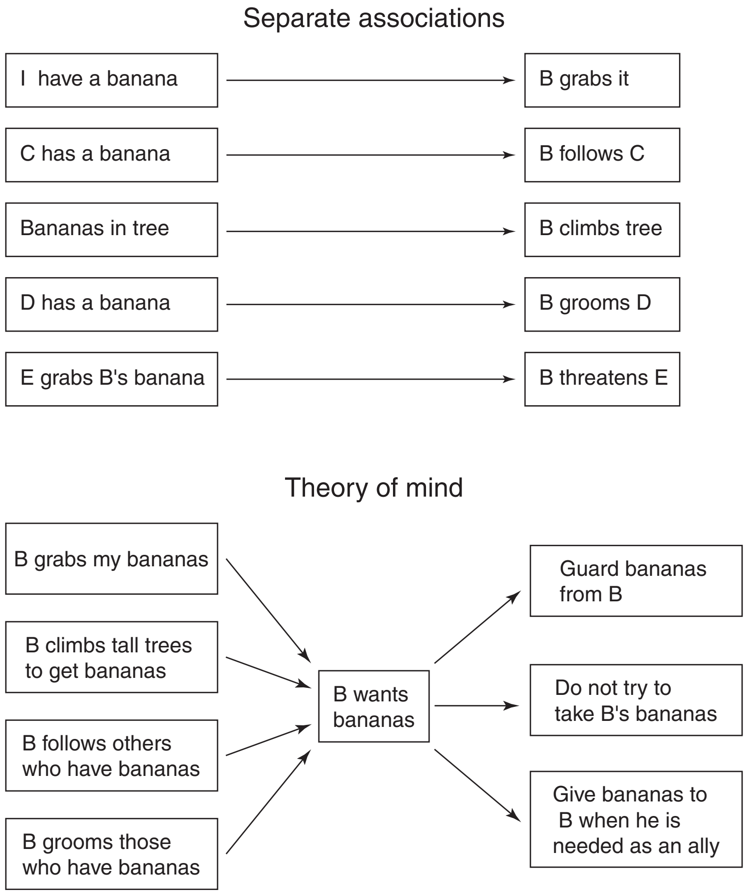


Figure 12.17. Theory of mind as an intervening variable or behavioral abstraction that integrates information in separate associations. After Whiten (1994) with permission.

should act appropriately in a variety of situations, including physically novel ones where simple stimulus generalization from past learning will not work. Such a device would be expected to evolve if it supports fitness-increasing generalization from one social situation to another (Seyfarth and Cheney 1994). For instance, seeing B climb tall trees for bananas and snatch bananas from others gives A no grounds to fear B as a banana thief if she cannot generalize from those physical situations to one in which B is watching when she is eating a banana. Folk psychology assumes that theory of mind mediates this generalization, but the representation in Figure 12.17 is equally consistent with what Povinelli and colleagues (e.g., Povinelli and Vonk 2004) call *behavioral abstraction*. To illustrate this distinction with the false belief test (Figure 12.11), a child who correctly identifies the box where the ignorant stooge will look might explain his answer by saying, “Because that’s where he saw it last” (behavioral abstraction) or “Because he thinks it’s there” (theory of mind). That is to say, the cognitive structure that connects perception and/or memory of others’ behaviors to one's own responses in Figure 12.17 need not be an explicit representation of others' states of mind (Sober 1998; Penn and Povinelli 2007b).

The information in this section so far indicates that through some combination of predispositions for reading and remembering species-specific behaviors and learning like that responsible for mediated generalization (Chapter 6) animals come to categorize behavioral cues together as relevant to given behavior systems or functionally related responses. Just as with physical events, memory for social events engages adaptively relevant behaviors. For example, corvids and chimpanzees treat an individual that gazes at or is remembered as gazing at a desirable piece of food as a competitor or perhaps the owner of the food (Burkart and Heschl 2007). This means that encountering that individual when the food is available to be retrieved engages a species-specific suite of defensive, functionally deceptive, or avoidant behaviors that vary flexibly depending on the spatial setup and the social status of the competitor. Similarly, when the male baboons in Bachmann and Kummer's experiment (Figure 12.2) had seen a particular male and female interacting in a friendly manner, they avoided contact with the couple rather than attempting to gain access to the female.

Inference from self to other

If behavioral abstractions can do the same job as theory of mind in all the tests described so far, maybe a new approach to isolating theory of mind is called for. One such proposed approach rests on a particular interpretation of human theory of mind, namely that it is based on inference—not necessarily explicit—from self to other. Such inference is of the form, "When I look toward something with my eyes open, I see it; when I grab something, I want it; therefore, when others like me do the same things, they must have the same mental states." In a proposed test of chimpanzees based on this notion (Heyes 1998; Penn and Povinelli 2007b), subjects would first be exposed to two distinctively colored visors attached to helmets of some sort. One, for example the red one, would be transparent and the other, for example the blue one, would be opaque. By putting them over its eyes the animal would learn that it can see through the red one but not the blue one. The test phase would resemble Povinelli and Eddy's tests sketched in Figure 12.12 except that people from whom the chimpanzee can beg would be wearing the visors. Choice of the person with the transparent visor would be evidence that the animal imputed its own experience of seeing to another individual.

Informal reports indicate that this has been tried with chimpanzees and they chose randomly (see Penn and Povinelli 2007b), whereas 12- to 18-month-old toddlers behave as if projecting their experience with an opaque or see-through blindfold onto an adult wearing it (Meltzoff 2007). However, not all agree that this would be a powerful test of theory of mind for chimpanzees. The animal need not use the visors' effects on seeing but on its ability to do things while wearing them in order to choose the person who could respond to its request (Andrews 2005; Penn and Povinelli 2007b). Moreover, notwithstanding that "self-recognition" in front of mirrors has been taken as evidence for theory of mind in chimpanzees (Box 12.3), whether the ability to generalize from self to other is predictive of behaviors consistent with theory of mind seems to be an empirical question.

Box 12.3 Monkey in the Mirror

When chimpanzees are exposed to mirrors, at first they treat the reflection like a conspecific, directing threat, greeting, and other social responses to it. Over a few days, social responses wane and self-directed responses emerge. As described by Gallup (1970, 86), who first systematically documented them, these include "grooming parts of the body which would otherwise be visually inaccessible without the mirror, picking bits of food from between the teeth while watching the mirror image, visually guided manipulation of anal-genital areas by means of the mirror," (Figure B12.3). To be sure the animals were referring the reflected image to themselves Gallup devised the *mark test.* The chimps were anesthetized and marked on one eyebrow and the top of the opposite ear with an odorless, non irritating, red dye. After recovering from the anesthesia, the animals showed virtually no behavior directed at the marks until the mirror was reintroduced. Then they touched and rubbed the marks, sometimes looking at their fingers or sniffing them in between touches. Two control chimpanzees that had never seen mirrors did not respond to the marks. In the same study monkeys of various species exposed to mirrors all behaved socially to the mirrors throughout exposure, and none of them touched marks above control levels during the tests. This finding has been repeated many times with a large number of monkey species. Other mammals, birds, and fish also treat mirrors primarily as conspecifics. But among apes, orangutans behave like chimpanzees, the available evidence indicates that bonobos do too, but gorillas do not (reviews in Povinelli and Cant 1995; Tomasello and Call 1997; de Veer and van den Bos 1999; Gallup, Anderson, and Shilito 2002).

How to interpret behavior toward mirrors is controversial. On one view (Gallup 1970; Gallup et al. 2002; Bekoff and Sherman 2004) the chimpanzees' behavior is evidence of self-awareness, and projection of this self-concept onto others underlies theory of mind. Reasons to doubt this interpretation include that—unlike healthy children—not all chimpanzees pass the mark test, the proportion that pass a first test declines with age (Povinelli et a1.1993), and self-directed behavior in front of mirrors does not necessarily predict either success in the mark test or "passing" tests of theory of mind. Moreover, theory of mind and behavior toward mirrors are sometimes dissociated in humans; children with autism appear deficient in their understanding of other people's mental states, but their behavior in front of mirrors develops normally (Povinelli 1996).

It is unlikely that nonverbal animals have a fully humanlike sense of self, and critics like Heyes (1994b) have wisely suggested their behavior be called not self-recognition but *mirror-guided body inspection,* a sophisticated kind of visual-kinesthetic matching, self-*perception* rather than self-*conception.* Why the ability to integrate visual, tactile, and proprioceptive input obtained in front of a mirror with the direct visual perception of self would evolve and be confined to great apes and humans is a puzzle. Any animal must use some sense of its own body to move around in the world without bumping into things. Pouncing on prey, leaping from branch to branch, flying through a forest, scratching an itch: all require at least a limited perception of the body's extent. Some birds, for instance, are reluctant to fly through a narrow gap, as if sensing the extent of their wings (Cuthill and Guilford 1990). One suggestion is that locomotion by clambering in early apes required more elaborate representation of the body (Povinelli and Cant 1995). In any case, experience with the mirror must allow the animal to form a visual representation of the parts of its body that it does not normally see, such as its face and ano-genital region, and integrate them with a representation it

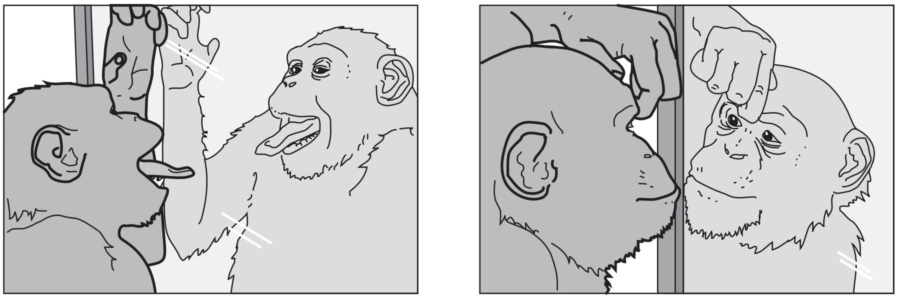


Figure B12.3. A chimpanzee engaging in self-exploratory behavior while looking in a mirror. From photographs in Povinelli and Preuss (1995) with permission.

already has based on tactile and proprioceptive feedback. This representation allows detection of a mismatch, as when dye is applied in the mark test, but then the animal must also be motivated to explore the altered parts of its body. It is not always clear whether such motivation is comparable across species in comparative studies in this area (de Veer and van den Bos 1999; Bard et al, 2006).

Nearly 40 years after Gallup's (1970) seminal article, most issues surrounding apes' "self-recognition" in mirrors are unresolved. There are still occasional reports of mirror-directed body inspection in other species (e.g., Plotnik, de Waal, and Reiss 2006; Prior, Schwarz, and Güntürkün 2008). Just as with apes, not all subjects of a given species "pass." With primates, new insights have been contributed by looking at specific elements of mirror-directed behavior in novel ways. Apparently for the first time with any species de Waal and colleagues (2005) directly compared the responses of mirror-naïve animals (capuchin monkeys) to a same-sex stranger in a neighboring cage, a familiar same-sex conspecific, and a mirror. The monkeys immediately showed more positive, friendly, responses and fewer threatening or anxious ones to the mirror than to the stranger. Thus although capuchins do not show mirror self-recognition, for reasons not yet understood the monkey in the mirror is not entirely a stranger either. And in a test of whether learning to use the mirror as a tool would enhance its use in self-grooming, Heschl and Burkhart (2006) trained marmosets to use a mirror to locate things (out-of-sight pieces of food) in the real world. Their skill did not transfer to marks on their heads. Indeed, when the mark was a dab of chocolate cream, rather than touching their own face, most of the animals tried to lick it off the mirror image.

By now, some readers may be inclined to dismiss the vexing question of what animals do in front of mirrors as overblown and misguided. Although animals in the wild may occasionally see their reflections in pools of water, how they behave toward them may not have much adaptive significance. Some intriguing connections have been made between mirror guided body inspection and other aspects of cognition, but it is still not clear that behavior in front of mirrors reflects any fundamental cognitive processes.

Behavioral abstractions

If theory of mind (or behavioral abstraction) allows its possessor economically to encode information and generalize about others' behavior, then any attempt to assess theory of mind must use more than one behavioral test. Moreover, the results of a set of such tests should be statistically nonindependent (Sober 1998). That is, passing one should predict passing others judged to be of similar difficulty. Heyes (1993b) has called this method *triangulation* because it is designed to point to the same conclusion from different metaphorical angles. Just as in any test of a concept (Chapter 6), in triangulation an animal acquires information in one set of conditions and is tested in conditions that are conceptually but not perceptually similar. Penn and Povinelli (2007b) have proposed a new series of false belief tests for chimpanzees based on this logic, using food competition. The proposed setup would be like that in Figure 12.13, but more locations for hiding the food would be available to permit discriminating each of two predicted choices from random behavior. Two locations per trial would be baited, each with a different amount of food. Subordinate subjects are trained to go for the smaller amount in direct competition with a knowledgeable dominant. Then they would experience an elaborate series of tests in which the competitor sees or does not see the food placed and the food is or is not moved or the two food amounts swapped when the competitor is or is not watching. Penn and Povinelli (2007b) suggest that combined results of their proposed tests could distinguish among various possible behavioral rules. Most importantly (see Heyes 2008), some of them would directly contrast predictions from theory of mind with predictions from specific plausible behavioral rules. As Penn and Povinelli acknowledge, however, their proposed protocol is complex and might be difficult to implement for that reason. Whether it ever will be remains to be seen.

Looking in the wrong places?

In the hypothetical tests just discussed, as in those that have actually been done, theory of mind is conceived as a device for predicting the behavior of others. The philosopher Kristin Andrews (2005) has suggested that such tests are "looking in all the wrong places" because humans use theory of mind not to predict others' behavior but to explain it verbally. Indeed, people often do not explicitly reason about others' mental states before acting but react unthinkingly to behavioral cues. This claim is in line with evidence that human theory of mind is closely tied to language, both during development (Perner and Ruffman 2005) and in adults as well. For example, when people watch a cartoon and do an interfering verbal or nonverbal task at the same time, their ability to answer a question about false beliefs of a character in the cartoon is selectively impaired by the verbal task (Newton and de Villiers 2007). This finding is consistent with evidence from tests of implicit memory (Chapter 7) that false beliefs are not tracked automatically, unlike true beliefs/the true state of the world (Apperly et al. 2006).

Andrews (2005) suggests that whether chimpanzees use theory of mind as explanation could be tested nonverbally with a variant of the colored visor experiment. After experience with the distinctive opaque and transparent visors, the chimpanzee would interact with other individuals wearing the visors, but now their color coding is reversed. If, for example, someone with the "transparent" visor behaves as if unable to see, the chimpanzee should find this surprising and perhaps seek an explanation. One acknowledged drawback of this proposal is that it is difficult to specify exactly what animals should do in such a situation and what would count as seeking an explanation. For example, increasing attention or looking are ways of getting information about something unexpected, but they would probably not count as explicit information-seeking.

12.4.5 Conclusions: Misled by folk psychology or denying continuity?

In the absence of evidence that chimpanzees pass a false belief test (see Kaminski, Call, and Tomasello 2008) or any other data agreed to discriminate conclusively between use of behavioral abstractions and reasoning about theory of mind, controversy in this area will surely continue. Are proponents of animal theory of mind being led too far beyond the data by their own folk psychology or are those who conclude that chimpanzees do not reason about mental states denying evolutionary continuity? Morgan's Canon (Chapter 1) is being severely tested here: maybe it's simplest to attribute humanlike theory of mind at least to chimpanzees and other great apes, though it's not clear where this line of reasoning leaves ravens and scrub jays.

One reply to this proposal is that there may be a genuine discontinuity here because human language underlies reasoning about others' states of mind in the first place. But evolutionary continuity is not all or none, especially not when it comes to such a multifaceted ability as theory of mind. Maybe human theory of mind is modular and only some aspects of it are shared by some other species (Lyons and Santos 2006). Indeed, very early on, Premack himself (see Emery and Clayton 2009) suggested three classes or subdivisions of theory of mind: understanding others' attention and perception, their desires and intentions, and their knowledge and beliefs. Much of the research reviewed here seems to have treated animal theory of mind as an all-or-nothing issue, but it is becoming clear that nonhuman species may share some but not all of these separate human competences. For example, the analysis of gaze-following summarized in Box 12.2 shows that many animals follow gaze in subtle ways but without necessarily understanding that the gazer is acquiring knowledge. A prominent suggestion of this kind is that chimpanzees and perhaps some other species understand others' intentions, or "understand others as intentional beings" (Tomasello, Call, and Hare 2003; Tomasello. et al. 2005; Cheney and Seyfarth 2007; Call and Tomasello 2008). However, one can "understand intentions" in the sense of predicting what others are about to do or try to do from behavioral cues such as what they are looking at or moving toward without understanding their underlying mental representations or goals. This latter kind of understanding could be useful in cooperating with others, but the next section—on cooperation—provides no more evidence for it than does this one.

12.5 Cooperation

12.5.1 The evolution of altruism

In behavioral ecology, *altruism* refers to behavior that increases the reproductive success of others at a cost to oneself. When selection can operate between groups, as is increasingly acknowledged (see Box 1.2), cooperative behaviors such as those to be discussed in Section 12.5.3 are expected, but on the view that the main force in evolution is individual selection, altruism is evolutionary puzzle: to be selected, behaviors need to increase the representation of the performer's own genes, not somebody else's. However, with individual selection alone altruism can still evolve under at least three conditions: *kin selection, mutualism,* and *reciprocal altruism* (Trivers 1971). Altruistic behavior directed toward relatives evolves through kin selection as long as those helped bear a large enough proportion of that individual's genes (see Section 5.4). Mutualism refers to cases in which unrelated individuals all concurrently achieve a net benefit from the interaction, as in "you scratch my back while I'm scratching yours." Thus its evolution is similarly unmysterious. When benefits are delayed relative to costs, as in "If you scratch my back now, I'll scratch yours later" or "If you scratch my back now, I'll support you in a fight later," we have reciprocal altruism.

Until relatively recently, kin selection, mutualism, and reciprocal altruism were thought to exhaust the conditions for the evolution of altruism (see West, Griffin, and Gardner 2007). Notice that these are functional terms. Their significance in evolutionary theory must not be confused with their cognitive or emotional implications: altruists need not experience empathy for those helped, nor as we saw in Chapter 5 do those helping kin need to understand relatedness. But each kind of altruism does have specific cognitive (Stevens, Cushman, and Hauser 2005) and emotional (Silk 2007c; de Waal 2008) implications. Kin selection implies discriminative behavior toward kin, which can arise through a variety of recognition mechanisms discussed in Chapter 5. It is easy to imagine that mutualism might be maintained by immediate reinforcement of participants' acts, and this supposition is sometimes correct. Reciprocal altruism has traditionally (e.g., Trivers 1971) been thought to be the most cognitively demanding because reciprocal altruists must recognize each other and remember each other's altruistic acts as if keeping sophisticated mental balance sheets. In addition, interactions of the form "If you scratch my back now I'll support you in a fight later" seem to imply behavior maintained by delayed reinforcement, which as we know from Chapter 11 is not very effective. As these considerations predict, there seem to be few good examples of reciprocal altruism (Stevens, Cushman, and Hauser 2005; Silk 2007d). Cooperative behavior can also be maintained by current punishment (*harassment*) of noncooperators or the threat of future punishment (*sanctioning*) for example, "If you don't scratch my back now, I'll take your food later" (Clutton-Brock and Parker 1995; Stevens, Cushman, and Hauser 2005). Sanctioning requires the same kind of memory for past interactions as reciprocal altruism and is accordingly rare (Stevens, Cushman, and Hauser 2005).

In this section we look first at a few examples of naturally occurring cooperative behavior for which there is at least a hint about underlying mechanisms (for more extensive discussion see Silk 2007d). We then look at new models of the evolution of human sociality showing how cooperative behavior can evolve under conditions not encompassed by classic models of altruism and at some experiments designed to test whether the mechanisms implied by these models are shared with any other primates.

12.5.2 Altruism in the wild

Mutualism

The example of mutualism probably the best-analyzed mechanistically is that among fish and their cleaners (Trivers 1971; Bshary 2006). Cleaner fish species subsist on the ectoparasites they eat from the surfaces of other fish. Cleaners closely approach their "clients," which may be larger predatory fish and even swim in and out of their mouths, but they are seldom eaten. Cleaners may have specialized coloration and behaviors that signal their approach; clients likewise have special behaviors of resting in a trancelike state while being cleaned and then signaling to the cleaner when they are about to depart. The client benefits by getting rid of parasites, and the cleaner gets a meal. Cleaners have fixed stations on the reef, which their clients visit regularly. Contact with cleaners is reinforcing for clients, which learn not the identity of their cleaners as such but the locations where they are found. In the laboratory, fish will learn to enter an area where they are contacted by a cleaner model (Losey 1979).

In the Australian reef fish studied by Bshary and his colleagues, cleaner wrasse, *Labriodes dimidaitus,* sometimes cheat by eating the client's mucus, a food they prefer to parasites. Clients respond by attacking the cleaner and/or swimming away. Bshary and Grutter (2005) simulated this interaction in the laboratory by letting Plexiglas plates coated with food play the role of clients. When both shrimp and fish flakes were offered, cleaners ate the shrimp first, but if an attempt to take shrimp from a plate caused it to "chase" them or "dart away," they learned to take flakes first. On the reef cleaners interact with clients up to 2000 times a day, so there would be plenty of opportunity for the learning demonstrated in this study to shape their behavior, even toward individual clients. Because clients evidently sense when a cleaner is eating mucus and find it aversive, they may also learn which cleaners are reliable. In effect, this would be an example of *direct reciprocity,* that is, one individual reciprocates a known other individual for past benefits or costs. Here it can result from associative learning through positive reinforcement and punishment (being attacked or having mucus eaten) or negative reinforcement (the client

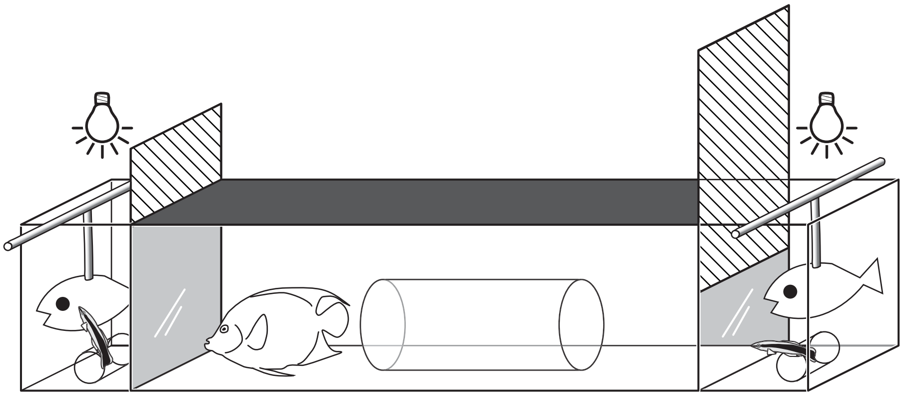


Figure 12.18. Setup in which a client fish, in the central compartment, eavesdrops through one-way mirrors on interactions of two cleaners (the thin black fish) with model clients. In the left end the cleaner appears to be cleaning the model, whereas in the right (nonpreferred) end the cleaner is just swimming around. After Bshary and Grutter (2006) with permission.

withdrawing). Current excitatory strength is in effect a tally of net value of past interactions with a particular client or cleaner. Any learning specializations here lie in the special events that reinforce or punish cleaners and clients.

Clients also learn about cleaners by eavesdropping on their behavior toward other clients (Bshary and d'Souza 2005). On the reef, clients more readily approach a cleaner if it has just been seen cleaning another client without conflict than causing it to dart away. In the laboratory setup shown in Figure 12.18, clients spend more than half their time near the end of a tank where a cleaner is eating from a Plexiglas model fish when the other end of the tank has a cleaner just swimming around, that is, with unknown behavior toward clients. In effect, such preference is an example of *indirect reciprocity,* in that cleaners who do not cheat are reciprocated for their cooperative behavior by eavesdroppers that in turn become their clients. Models like those sketched in Section 12.5.3 show that indirect reciprocity can evolve in species with social networks in which individuals acquire an *image score* or reputation. Those seen to be good cooperators are reciprocated by being cooperated with. So far in the cleaner-client system such image scoring has been shown only to affect immediate choice between waiting a turn at a given cleaning station or going elsewhere. As one might therefore expect, cleaners are more cooperative when they have an audience (Bshary and d'Souza 2005), another likely effect of reinforcement contingencies that has been reproduced in the laboratory (Bshary and Grutter 2006).

Reciprocal altruism in vampire bats?

Unlike mutualism, in reciprocal altruism acts are exchanged over delays. A much-discussed candidate involves vampire bats (*Desmodus rotundus*). Vampires fly out each evening from communal roosts to seek a meal of blood. A substantial blood meal allows a bat to survive another 50–60 hours before feeding again, but not every bat succeeds in getting a meal every night. Unfed bats may starve within 24 hours, but a starving bat can be rescued if a recently fed bat regurgitates blood for it. To test whether feedings were reciprocal, groups of unrelated bats were kept in the laboratory, and each night one was kept without food while the others fed (Wilkinson 1984). When the hungry bat was returned to the group, in 12 of 13 cases it was fed by another bat from the group it had come from in the wild. Moreover, the recipients of regurgitations tended to reciprocate the donation on a later night. These observations suggest that vampire bats recognize unrelated individuals and retain some memory of past interactions with them. However, the relatedness of the bats involved was not always known; because some may have been closely related the possibility remains open that the behavior is kin selected (Stevens, Cushman, and Hauser 2005).

Cooperative sentinels?

Some group-living species appear to resolve the conflict between feeding and vigilance as humans might, by posting sentinels who watch for predators from an exposed location while others forage. At first glance, reciprocal altruism might be in operation here to ensure an equitable sharing of dangerous guard duties. However, it turns out that at least for meerkats not only is a basic assumption of this theory wrong—guards are less vulnerable to predation than their busily foraging companions, not more—but there is no regular rotation of sentinels as would be expected if opportunity to feed is regularly being repaid by time on guard. Instead, meerkats are more likely to guard when they are near satiation (Clutton-Brock et al. 1999). Individuals experimentally given extra food guarded more often and for longer, and individuals that were unusually hungry because they had been babysitting at the burrow temporarily guarded less. Here, then, a simple kind of social organization arises from largely individual processes. A meerkat's top motivational priority is feeding; once fed, it will guard if no one else is on guard at the time.

Reciprocity and alliances in wild primates

As we saw in Section 12.2, members of a primate troop have friendly relationships expressed in mutual grooming and support in agonistic interactions. Such observations suggest the participants are reciprocal altruists who are exchanging grooming for agonistic support (see Silk 2007d). Indeed this does seem to be the case in a group of captive Japanese macaques studied by Schino, Sorrentino, and Tiddi (2007). They analyzed a large number of grooming and agonistic interactions, statistically removing effects of kinship and proximity, and found that not only did monkeys groom most those that had groomed them most, they also groomed most those individuals that had supported them most. Support was similarly predicted by past receipt of both support and grooming. The relevant correlations were apparent over the long term but not when only events in the past 30 minutes were analyzed. The fact that, for example, grooming monkey A today is repaid by A's support tomorrow or the next day seems to imply either learning over long delays or a detailed memory of specific interactions. The improbability of either has been claimed to be a cognitive constraint on reciprocal altruism (Stevens, Cushman, and Hauser 2005). However, as with the cleaner fish, the net effect of past interactions with a particular individual can just as well be encoded as a single current value or attitude, similar to associative strength in models of learning (Chapter 4), resulting in what de Waal (2000) calls *attitudinal reciprocity*. As nicely put by Schino et al. (2007, 186) "it is necessary to assume only that the exchange of services triggers partner-specific emotional variations and that monkeys make their behavioral decisions on the basis of the emotional state associated to each potential partner."

12.5.3 Cooperation and other-regarding behavior

The evolution of human cooperation

Cooperation is a hallmark of human society. Not merely do people behave considerately toward complete strangers, they sometimes make substantial financial and even physical sacrifices for them. Such behavior seems impossible to explain with classic models of the evolution of altruism in which cooperation between unrelated others can arise only when the same individuals interact repeatedly. However, new models of the evolution of human sociality and the results of experiments to test them suggest that a sense of fairness and other foundations of morality have deep evolutionary roots. Such models consider processes at the level of groups of individuals, but without relying on the discredited notion of group selection in which individuals act "for the good of the group" (Wilson and Wilson 2007, 2008). Genes promoting prosocial tendencies in individuals can arise when groups compete in ways argued to be characteristic of the early stages of human evolution. In particular, such conditions may have promoted the evolution of *strong reciprocity,* a tendency to cooperate with anonymous unrelated others and to punish those who do not do the same even when doing so is costly to the punisher (Nowak 2006; review in Gintis et al. 2007).

A good deal of the evidence that people actually have such tendencies comes from simple stripped down social situations, economic games, a key one of which is *the ultimatum game.* The rules are as follows. One individual, the *proposer,* is given a sum of money, say $10, to divide between himself and an anonymous stranger, the *responder.* He can offer the responder any amount from $1 to $10, and if the responder accepts, they both keep whatever is proposed; if the responder rejects, they both get nothing. In either case, they do not interact again. Notice that because the players are anonymous and interact only once, neither one's behavior should be influenced by expectations of the other's approval, reciprocation, or retaliation. Because it should be obvious to both players that the responder will do better by accepting any proposal than rejecting it, selfish proposers should consistently make very low offers and responders should accept them. But contrary to these expectations, proposers generally offer more than the minimum, often near 50% of the total on average, and responders reject very low offers, a costly act that punishes the proposer. Indeed, people report feeling angry at very low offers. There are differences among individuals and also across cultures (see Gintis et al. 2007), but the findings are clearly better described as strong reciprocity than as uniformly self-regarding behavior (i.e., behavior that maximizes the actor's own gain in the short run). These developments have stimulated tests of whether monkeys or apes show such prosocial or other-regarding tendencies, that is do they seem to have a sense of fairness or cooperate with unrelated others? Or is strong reciprocity a uniquely human trait?

Inequity aversion: Do monkeys have a sense of fairness?

One of the first and most controversial tests of other-regarding behavior in primates was a study by Brosnan and de Waal (2003; see also van Wolkenten, Brosnan, and de Waal 2007) with capuchin monkeys. The capuchins had learned to exchange tokens (small rocks) for food. The experimenter would give the monkey a token, and then offer food which the monkey could obtain by handing back the token. In the main experiment, two capuchins in neighboring cages could watch each other engaged in this game; importantly, each could see if its neighbor was getting a grape (a preferred

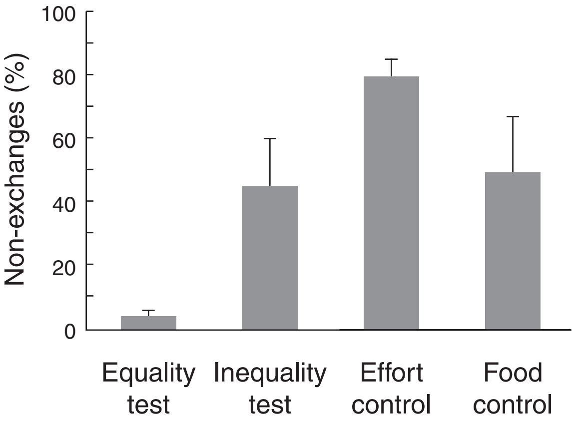


Figure 12.19. Proportion of trials in which subject monkeys refused to exchange a token for a piece of cucumber when a neighbor was getting cucumber (Equality test) or a preferred grape (Inequality test). Control conditions are described in the text. After Brosnan and de Waal (2003) with permission.

food) or a cucumber slice (a nonpreferred food) for its efforts. Isolated capuchins would play for cucumber, but seeing its neighbor get a grape greatly increased a capuchin's tendency to reject cucumber (Equality vs. Inequality tests in Figure 12.19), a phenomenon Brosnan and deWaal called *inequity aversion*.

But what is really going on here? To some extent cucumber is simply less attractive in the presence of grapes irrespective of whether the grapes are being received by another animal (Wynne 2004b). The data from two control conditions in the original study provide evidence for such a contrast effect (Figure 12.19). When a grape was either given to the neighbor for no effort or simply placed in the empty neighboring cage (Effort and Food controls in Figure 12.19), failures to exchange were elevated about as much as when the partner "received unequal pay for equal work." A less immediately obvious source of contrast is that many of the trials in which monkeys rejected cucumber occurred after trials in which those same subjects received grapes (Brosnan and de Waal 2006; Roma et al. 2006). Moreover, although the original report of this effect (Brosnan and deWaal, 2003) was called "Monkeys reject unequal pay," the "work" implied by the title seems trivial. Handing the experimenter a token hardly seems to require more effort than reaching out for food, and accordingly the role of "work" in the effect is also debatable (Fontenot et al. 2007; van Wolkenten, Brosnan, and de Waal 2007). Finally, what is being claimed here? Some discussions of inequity aversion seem to suggest that monkeys have a humanlike emotional reaction to unfairness (cf. Brosnan and de Waal 2003; Wynne 2004b). A more measured interpretation (e.g., Silk 2007c) is that sensitivity to differences between one's own rewards and those available to others could be one of the evolutionary building blocks of human responses to unfairness. Which nonhuman primates show such sensitivity and under what conditions remains to be better understood.

Are chimpanzees altruistic?

Whatever else is going on in tests of inequity aversion, subjects seem averse only to getting less than a companion (Henrich 2004). Getting more than a companion, an equally unfair allotment, does not seem to bother them, whereas tests like the ultimatum game suggest that people are averse to any form of inequity. Another line of research supports the same conclusion. Here, food is out of reach outside a cage, and primate subjects can use a rope or handle to pull it in. If at the same time they can move additional food toward a second animal, do they choose this altruistic act over delivering food to themselves at the same cost? Tests of chimpanzees from several captive groups answer this question resoundingly in the negative (Silk et al. 2005; Jensen et al. 2006; Silk 2007d; Vonk et al. 2008). In each case, chimpanzees could choose to operate either of two pairs of trays. Trays in one pair had a piece of food for the subject and one for a familiar group member in a neighboring cage; the other pair of trays had food for the subject and an empty tray for the neighbor. Subjects were indifferent between these options. They similarly chose only on the basis of personal gain when one choice prevented delivery of food to another (Jensen. et al. 2006).

One of the most clever and elaborate illustrations of chimpanzees' pure self-regard and apparent insensitivity to fairness in such situations is the behavior of pairs of animals in a simplified ultimatum game (Figure 12.20; Jensen, Call, and Tomasello 2007). Again one animal, here in the role of proposer, chose between two pairs of trays. Each pair had 10 raisins, but they were allocated differently between the proposer's tray and the responder's. For example, the choice might be between an 8:2 allotment and 5:5. The proposer could pull one tray closer to both animals, and the responder could then complete the delivery of the chosen raisin allotment to both or reject it. Proposers preferred options with more for themselves, and as long as they got at least one raisin, responders hardly every rejected any offer no matter how inequitable. Control procedures showed that the animals could see what their companion was getting and could discriminate among the amounts of food offered. Unlike in an earlier study that provided some (albeit weak, Stevens, Cushman, and Hauser 2005) evidence for altruistic choices in cotton top tamarins after extensive training (Hauser et al. 2003), here the animals had comparatively few trials with a given condition and companion. Thus, even though the interaction was not anonymous as it usually is with humans in the ultimatum game, it came close to testing the animals' spontaneous preferences, and in any case repeated interactions with known individuals would have been expected to increase displays of fairness. It can be argued that other factors besides species difference such as the desirability of the food reward contributed to the difference between these findings and those that would be expected for humans, but they are consistent with the conclusion that chimpanzees do not

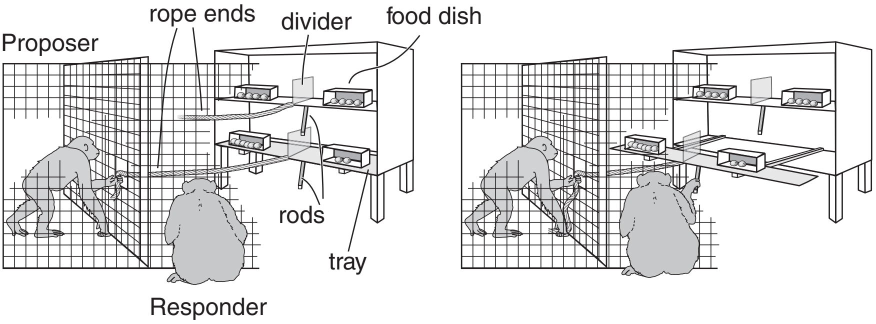


Figure 12.20. Ultimatum game for chimpanzees. On the left, the proposer chooses between the upper and the lower trays, each of which holds pair of food dishes with a different allotment of a fixed number of raisins (here 8). On the right, the proposer has pulled the lower tray so its rod is within reach of the responder, who can complete delivery of the chosen allotment, for example, 6 raisins to the proposer and 2 to himself. After Jensen, Call, and Tomasello (2007) with permission.

share our sense of fairness but are concerned only with maximizing their own economic gains (Jensen, Call, and Tomasello 2007).

Do chimpanzees and monkeys cooperate?

Of course maximizing individual gain is not inconsistent with cooperating in mutualistic situations, particularly those that involve large rewards not easily obtainable by individuals acting alone. Indeed, some chimpanzees are wonderful cooperative hunters. Boesch and Boesch-Acherman (2000) vividly describe how males in the Tai forest go after colobus monkeys, some driving a potential victim down from the trees while others wait on the ground. The animals are clearly cooperating in a complex way, but because skilled hunting takes up to 20 years to develop, it is difficult to say exactly what cognitive skills they are using and how they come to use them. This issue is addressed by experiments in which pairs of apes or monkeys are presented with tasks in which they must act together on an apparatus like that in Figure 12.21 to obtain reward (review in Noë 2006; Silk 2007d). Of course it is not at all surprising if one animal can use another's behavior or the results of it as a discriminative stimulus in a learning task. The questions about specifically social cognition here are therefore something like the following. Do animals ever cooperate spontaneously? If so what animals under what conditions? Even if animals must learn to cooperate, are there specific cognitive prerequisites such as a tendency to attend to others' behavior or to give communicative signals? Or are the prerequisites primarily emotional or temperamental?

Tests of cooperation with brown and tufted capuchins in different laboratories have produced mixed results (see Noë 2006). These tolerant monkeys seem to cooperate in the wild, and they can learn cooperative tasks in the laboratory. Attending to the partner's behavior may contribute to solving them, in that blocking the view of the partner degrades performance (Mendres and de Waal 2000; but see Visalberghi, Pellegrini Quarantotti, and Tranchida 2000). Chimpanzees can also learn to pull such an apparatus together, but they seem to do so entirely through learning the contingencies between their own and the partner's behavior. Unlike in

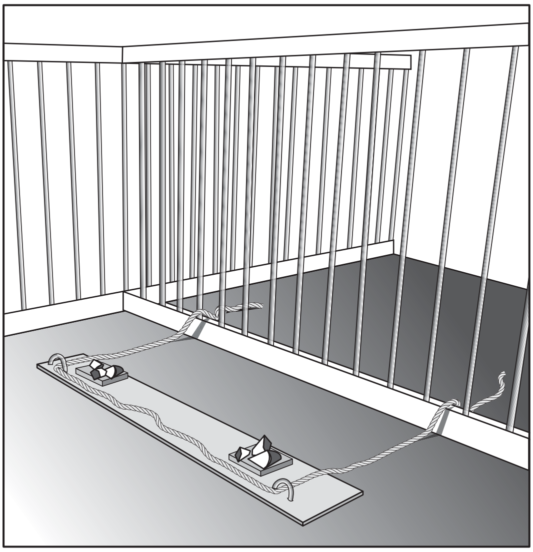


Figure 12.21. Apparatus for testing cooperation between two chimpanzees. Because the rope is not fixed firmly to the board holding the two food dishes and the ends are too far apart for one animal to reach both of them, getting the food within reach requires two animals to pull simultaneously, one on each end. After Melis, Hare, and Tomasello (2006a) with permission.

one case where the partner was a human (Hirata and Fuwa 2007), they do not attempt to induce cooperation with communicative signals and gestures. Importantly, even when chimpanzees' actions result in separate food for each animal, as would be the case with the apparatus in Figure 12.21, they succeed more often when working together with a partner that they more readily share food with in independent tests (Melis, Hare, and Tomasello 2006b). As this finding predicts, bonobos, which are more socially tolerant, are more successful than chimpanzees on this task (Hare et al. 2007), again supporting the notion that emotional or temperamental rather than specifically cognitive attributes underlie species differences in cooperation.

Empathy and the evolution of helping

The findings sketched so far all seem to point to the conclusion that regard for others' welfare is a uniquely human trait, evolved since humans and apes separated from their common ancestor, possibly in response to the conditions in early human social groups (Silk 2007c). Insofar as regard for another's welfare requires sensitivity to what they are thinking or feeling, this conclusion is entirely consistent with the lack of evidence for theory of mind in chimpanzees. But to some (de Waal 2008) this conclusion flies in the face of countless observations that in naturalistic social groups chimpanzees seem to empathize with others in distress. For example, an animal that has witnessed a fight may appear to console the loser by putting an arm around the loser's shoulders. Moreover, in experimental settings chimpanzees do respond spontaneously to signals that a conspecific or a person needs help, for example handing them an object that they are unsuccessfully reaching toward. Young children do the same thing (Warneken and Tomasello 2006; Warneken et al. 2007).

These situations differ in two important ways from the economic games in which chimpanzees fail to show regard for others: neither food nor learned responses are involved, and natural responses to natural signals are. Evolution may have produced proximate mechanisms for species-specific helpful behaviors in response to specific sign stimuli from body language or vocalizations (de Waal 2008). Responses like those described as consolation or helping may even be accompanied by humanlike affect, but such affect, if present, apparently cannot support functionally similar behavior such as delivering food to another via arbitrary learned responses. Indeed, a wide variety of species show emotional contagion, that is, seeing a conspecific in a certain emotional state arouses the same emotional state in the witness. For example, in the company of a mouse in pain, other mice exhibit a lower threshold to react to a painful stimulus, an effect that could be described as empathy (Langford et al. 2006). As we see in Chapter 13, such reactions can support witnesses' learning what caused their companions' distress.

In conclusion, whether or not animals cooperate or help others depends on not only the species but on what is meant by *helping* or *cooperating*. Animals can learn to cooperate in various ways, but it seems that self-interest generally prevails when small amounts of food are involved. However, some group-living animals actively signal the availability of large amounts of shareable food. Examples include ravens (Heinrich 1989) and the food-calling chickens discussed in Chapter 14. Mechanisms underlying apparent cooperation in such species might repay further analysis. In any case, looking for signs of altruism only in economic, food-related, decisions fails to recognize the importance of what de Waal (2008) calls the altruistic impulse, the spontaneous display of species-typical helpful responses. Rather than resulting from a conscious calculation of benefits to others, helping may be an unconscious reaction to sign stimuli. Such responses are surprisingly important even in human social life. As an example, when a photograph of eyes was placed beside the box where people placed contributions to a coffee pool, payments more than doubled compared to weeks when flowers were present instead (Bateson, Nettle, and Roberts 2006; Milinski and Rockenbach 2007).

12.6 Summary

In the course of the chapter we have seen evidence for a number of specifically cognitive mechanisms, some of them very simple. Many species respond to the gaze of conspecifics and/or predators, perhaps tracking the direction in which they are looking and/or using gaze as a cue to search behind barriers. Some primates and birds also retain this information for use in later competitive encounters. Response to gaze is thus a phylogenetically widespread component of social cognition. Human babies and most likely some other primates (at least) share a second such low-level component of social behavior, namely a propensity to respond to self-propelled objects as if they are animate and goal-directed. In the next chapter we see evidence for another candidate component of social cognition in the responses of mirror neurons in primate brains.

We have also encountered three candidates for higher level components of social cognition. Although it turns out, contrary to earlier suggestions (Tomasello and Call 1997), that sensitivity to third-party social relationships can be demonstrated in nonprimates including fish and birds, some primates classify their social companions in multiple ways simultaneously, perhaps using an ability for hierarchical classification that goes beyond anything yet demonstrated in laboratory studies of categorization in any species. This ability may go along with a particularly fine-tuned ability to decode social relationships. At the same time, however, there is as yet no evidence in any nonhuman species for two other important human social cognitive abilities—theory of mind and a sense of fairness (or a propensity to take other individuals' welfare into account in economic decision-making).

The focus of this chapter has been very much on primates, often on our closest living relatives, the chimpanzees. In the case of social knowledge this reflects the primacy of field research on primates in suggesting that social knowledge and social brains are special. While this conclusion may still prove to be correct, research has been tempering it with studies of species as diverse as hyenas, geese, and fish. Similarly, in research on the mentalistic aspects of social cognition, studies of chimpanzees together with those on young children originally predominated, but research has more recently moved on to look at other primate species as well as birds. To some extent the focus here on chimpanzees and other primates reflects a compelling interest in the question of what makes us human. Indeed, the early years of the twenty-first century have seen a veritable epidemic of attempts to characterize human cognitive uniqueness (e.g., Premack 2007; Penn, Holyoak, and Povinelli 2008). Based on the evidence in this chapter we might conclude that only humans have theory of mind or understand the unseen causes of social events just as they understand unseen physical causes. The final section of this chapter adds to this tentative catalog of species differences the suggestion that only humans govern economic decisions with a sense of fairness or understand the sufferings of others. Chapters 13 and 14 suggest further candidates for human uniqueness. But there are many reasons to doubt that the question "What makes us human?" has a simple answer. We look at it again in Chapter 15.

Further readings

Much of the material in this chapter is covered in more depth in the books edited by Emery, Clayton, and Frith (2007), de Waal and Tyack (2003), P. McGregor (2005), and Dunbar and Barrett (2007); in *Baboon Metaphysics* by Cheney and Seyfarth (2007); and in the review by Emery and Clayton (2009). A comprehensive review of dog behavior and cognition is the book by Miklosi (2007); the research bearing on theory-of-mind-like behaviors in dogs is comprehensively reviewed and analyzed in the article by Reid (2009). The most recent stances of those on two sides of the chimpanzee theory of mind debate are represented in the articles by Call and Tomasello (2008) on the one hand and Penn and Povinelli (2007b) on the other. Healy and Rowe (2007) is recommended for an analysis of the social brain and related proposals, Emery (2000) for a thorough review of social gaze and its neurobiological basis, and de Waal (2008) for a stimulating review of altruism.

13

Social Learning

In the past 50 years or so, forests of Jerusalem pine have been planted in Israel. Here black rats occupy the niche occupied by squirrels in other parts of the world, making their nests in the trees and eating pine seeds. Jerusalem pine seeds are protected by tough overlapping scales tightly wrapped around the central core of the pine cone. To obtain them efficiently, rats must strip the scales off the cones from bottom to top in a spiral pattern (Figure 13.1). Black rats do not learn by themselves to extract the seeds in this way, nor do isolated young rats, but young rats growing up in the pine forests do develop efficient stripping (Terkel 1995).

White-crowned sparrows (*Zonotrichia leucophrys*) are small songbirds, widely distributed in North America. Although they are a single species from Atlantic to Pacific, the songs sung by males during the breeding season vary from one region to another. In California, for example, there is a recognizable Berkeley dialect and a Sunset Beach dialect less than 20 miles away (Marler and Tamura 1964).

Different populations of wild chimpanzees depend on different foods, and they use tools to get some of these foods (Whiten et al. 1999). The chimpanzees of Gombe, in Tanzania, gently poke grass stems into termite mounds to extract the insects. Chimpanzees in the Tai Forest of the Ivory Coast open rock-hard coula nuts by placing them on a stone "anvil" and striking them with a smaller stone, which they may carry around with them. Young chimpanzees accompany tool-using adults and appear to watch them intently.

In all these examples, individuals seem to be learning from others in their social group. But if they are learning from one another, precisely what are they learning, and how are they learning it? Are there specialized mechanisms for social learning and, if so, are they better developed in species that live in groups? Should the localized groups of animals that share pine cone stripping, song dialects, or nut cracking be viewed as animal cultures? What can laboratory studies of social transmission mechanisms tell us about how animal traditions arise and spread?

Observations of animals apparently learning from one another raise both mechanistic and functional questions. In the past, the answers to these questions were pursued in two separate research traditions (Galef 1988; Whiten and Ham 1992). Beginning in the days of Darwin and Romanes, the primary mechanistic, or psychological, question about social learning was whether animals can imitate, that is, whether they can come to perform an action as a result of seeing it done. In contrast, anthropologists and behavioral ecologists have been more interested in discovering

Figure 13.1. Mother black rat and her pup feeding on pine cones. After drawings and photographs in Terkel (1995), with permission.

the conditions under which behaviors spread through populations and are maintained from generation to generation. In this context, mechanisms are important only as they determine the conditions under which behavior is transmitted. The last 20 years or so have seen increasing integration of the many perspectives on social learning (Zentall and and Galef 1988; Heyes and Galef 1996; Galef and Heyes 2004). For example, studies of imitation in chimpanzees and other nonhuman primates now intersect both with evolutionary models suggesting that a "ratcheting up" of culture is possible only in species that imitate (Richerson and Boyd 2005) and with investigations of mirror neurons in primate brains (Section 13.3).

Social learning refers to any learning resulting from the behavior of other animals (Box 13.1). Galef and Giraldeau (2001) characterize the two major approaches to studying it as "top down" (ecological or functional) and "bottom up" (psychological or mechanistic). This chapter begins with the former, with instances of social learning in naturalistic or seminaturalistic situations. In the central part of the chapter, on the

Box 13.1 A Social Learning Glossary

Social learning embraces such a potentially bewildering (C. M. Heyes 1993a) variety of different terms that a glossary is useful for keeping track. This one includes those most often encountered in contemporary discussions (Zentall 2006; Hoppitt et al. 2008). Historically, there have been many more, often with overlapping meanings (Galef 1988; Whiten and Ham 1992).

To begin with, any form of social learning requires an *observer* (or *actor)* and a *demonstrator,* who performs the behavior later reproduced in whole or part by the observer. To qualify as learning rather than socially elicited or facilitated behavior, the observer's performance must take place at a later time, away from direct influence of the demonstrator.

Copying. A generic term for doing the same thing as a demonstrator, mechanisms unspecified; for example copying another's choice of mate or foraging patch (Section 13.1).

Social facilitation. Individuals are more likely to perform a behavior when in the company of others performing it. For example, yawning is socially facilitated in people (Provine 2005).

Local enhancement/Stimulus enhancement. Increased likelihood of visiting a place (local enhancement) or contacting a type of stimulus (stimulus enhancement) by virtue of observing others doing it. The enhanced attractiveness of the location or stimulus may or may not be confined to times when demonstrators are present.

Observational conditioning. Associating a cue or object with an affective state or behavior(s) by virtue of watching demonstrators respond to it. For example (Section 13.2), having seen other birds mob an owl, an observer later responds to an owl by mobbing. Sometimes extended to cases in which the observer is directly reinforced following a cue or signal by the demonstrator as when parent babblers "purr" before feeding their young (Section 13.4). However, this seems to be direct conditioning of the observer, that is, CS = purr, US = food, CR = approach.

Imitation. Performing the same action as a demonstrator *by virtue of having seen the action performed.* The action must be novel, thus ruling out such phenomena as "mate choice copying."

Emulation. Copying only elements of a complex action. For example, having seen a demonstrator skillfully use a rake to pull food toward itself, an observer picks up the rake backwards and waves it in the general direction of the food. May be qualified by reference to the element of the sequence apparently emulated, as in *goal emulation* (Section 13.3).

Learning affordances. Learning what can be done with objects or parts of the environment, not necessarily through observing the actions of another animal. For example, an observer seeing a door opened by the wind may learn that it can be opened (*affords opening*).

"bottom up" approach, we see that processes other than imitation play the major role in most natural examples of social transmission. Indeed, much socially influenced learning does not appear to depend on any specialization for social learning as such but rather on species-specific perceptual and motivational mechanisms together with associative learning. Imitation (Section 13.3) may be an exception. At the end of the chapter we return to social learning in natural contexts with two contentious questions: Do animals teach (Section 13.4)? And can animals ever be said to have culture (Section 13.5)?

13.1 Social learning in context

13.1.1 Social transmission of food preferences in rats

One advantage of group living is that individuals foraging together may help each other find food. They may be attracted to feeding conspecifics, or they may follow others, as ants follow each other along chemical trails. Colonies or roosting places may serve as information centers where individuals inform each other about good foraging opportunities in the neighborhood. At one time information exchange was hypothesized to be a major factor in the evolution of sociality, but this *information center hypothesis* is now considered to be without broad empirical support (see Galef and Laland 2005). Nevertheless, information exchange is a potential benefit of sociality, and there are some good examples of animals using information about food sources provided by others in their colonies. Bees communicate the locations of nectar (Chapter 14), and as we see next, rats provide other rats with information about the flavors of edible foods.

Norway rats (*Rattus norvegicus*, the common laboratory rat) are colonial omnivores. They can and will eat almost anything that does not poison them. This means that young rats have a lot of potential foods to learn about, and they start learning before they are born. The flavors of foods eaten by a mother rat late in pregnancy influence the food preferences of her offspring when they begin to feed on solid food (review in Galef 1996b). The pups continue to learn from their mother when they are suckling because the flavors of foods she ingests are present in her milk. In addition when the weanling rats begin to leave the nest to forage, they prefer to forage where other rats are or recently have been feeding. Thus the young rat has at least three ways to become familiar with the flavors of foods being eaten safely by its mother and others in its colony. Combined with a preference for familiar over novel flavors, they almost guarantee that a young rat will eat things that are good for it, or at least not harmful.

In addition to choosing familiar flavors, both young and adult rats choose foods being eaten by their companions over alternatives. This was discovered in experiments designed as depicted in Figure 13.2 (Galef and Wigmore 1983). Pairs of rats lived together for a few days, eating normal laboratory rat chow. Then one rat in each pair, the *demonstrator,* was removed to another cage and deprived of food for 24 hours before being fed cinnamon or cocoa flavored chow. Next, each demonstrator was returned to its familiar companion, the *observer* rat, and demonstrators and observers interacted in the absence of food for 15 minutes. For the following 24 hours the observer, alone once again, had two bowls of food, one flavored with cinnamon and one with cocoa. As shown in Figure 13.2, during this time observers whose demonstrators ate cinnamon consumed more cinnamon-flavored food relative to cocoa flavored food than those whose demonstrators ate cocoa. A large

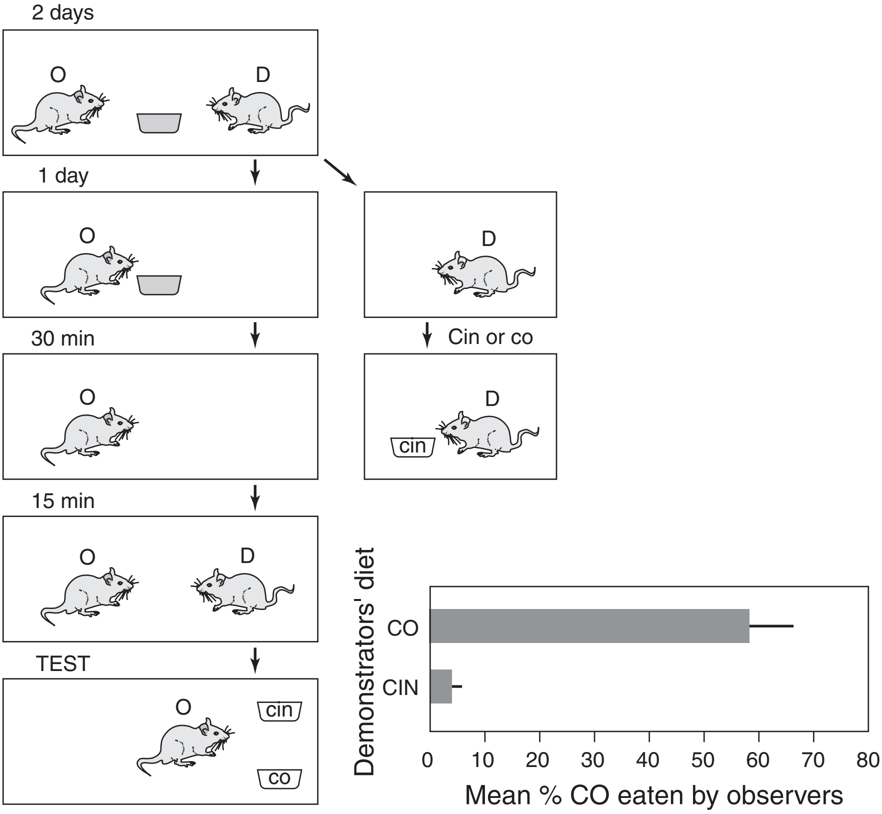


Figure 13.2. Design and results experiments establishing social transmission of food preferences in Norway rats. D = demonstrator; O = observer; CO = cocoa-flavored food; CIN = cinnamon-flavored food. Data are grams of CO eaten as a proportion of total consumption in the first 12 hours of the test in groups whose demonstrators ate CIN (as in the example portrayed) or CO. After Galef and Wigmore (1983) with permission.

number of related experiments has shown, among other things, that observers can be socially induced to choose a familiar food that a demonstrator has eaten recently and to seek out a place where that food is available (Galef 1996b). Thus rats apparently can, in effect, exchange information about what foods are currently available nearby, although the role of these processes in directing food choice in wild colonies is unknown. Such learning is also found in other rodent species (Galef 2007).

How do demonstrators communicate about food? A rat that has just been eating might carry bits of food on its fur and whiskers, but that is not all the observers detect. Observers need to smell the flavor on another rat's breath, more specifically in association with carbon disulfide, a prominent component of rat breath (Galef 1996b). Rats behave in a way that facilitates this learning: when they encounter one another they engage in mouth to mouth contact and sniffing. To borrow a term from embryology (Waddington 1966), development of food preferences in rats is *canalized:* in a kind of fail-safe system often found in development, several separate mechanisms independently and redundantly ensure that young rats will eat what others in their colony are eating.

The social learning mechanisms available to adults are sufficient to transmit colony members' acquired food preferences to succeeding generations (Galef and Allen 1995). In one example colonies of four rats were induced to prefer either Japanese horseradish or cayenne pepper flavored food by making them ill after they ate the alternative diet. The rats in these "founder" colonies were gradually replaced with naive rats until the colonies were made up entirely of rats that had never been poisoned after eating either of the diets. Nevertheless, rats in each colony were still preferring their colony's "traditional" diet. In one experiment, the tradition was maintained over four generations of replacement rats. Preference was still transmitted even when the new colony members never fed in the presence of the older members but just interacted with them in the hours between daily feedings.

13.1.2 Producing and scrounging: Social transmission of feeding techniques in pigeons

Baby rats represent a special case in which social learning is undeniably useful. Without influences from their mother and other adults, they would have to choose foods randomly once they were weaned. But in a group of adult animals encountering unfamiliar resources, not everyone should be engaging in social learning. Indeed, this would be an impossible situation: for there to be anything to learn socially, someone has to be acquiring information for himself, that is, engaging in *individual learning*. Thus when there is new information to be acquired, some should learn for themselves while others copy (Giraldeau, Valone, and Templeton 2002). And if a given individual already has an effective behavior for the situation, copying may not be his best policy. This informal functional notion suggests that animals might not always acquire a novel behavior being exhibited by another group member. The research of Louis Lefebvre, Luc-Alain Giraldeau, and their colleagues with captive and free-ranging pigeons (*Columba livia*) provides some of the best evidence for this suggestion.

Like rats, pigeons are highly social opportunistic foragers that are widely associated with humans because of their ability to flourish in a variety of conditions. Pigeons in the laboratory learn some novel feeding techniques more readily if they have seen them used by another pigeon than otherwise.

One such technique is pecking through a paper cover on a food dish. Pigeons that watch demonstrators both pierce the paper and eat grain perform the task themselves sooner than pigeons given partial demonstrations or no demonstrations (Palameta and Lefebvre 1985). However, when a skilled paper piercer was placed in a laboratory flock of ten birds, only four learned the skill. The others *scrounged* food uncovered by the birds that pierced (Lefebvre 1986). In contrast, when a trained demonstrator was introduced into a free-flying flock in Montreal, 24 birds learned to pierce on their own and only four specialized in scrounging. The sample sizes here are just one captive and one free-living flock, but Lefebvre and Palameta (1988) suggest that one reason for the great difference in proportion of learners is that because individuals could come and go from the urban flock, scroungers sometimes found themselves without anyone to scrounge from and had to learn for themselves to produce food from the apparatus.

In free-ranging flocks different individuals may specialize in different food-finding skills and change roles from producer to scrounger as the situation changes (Giraldeau and Lefebvre 1986). Opportunity to scrounge may reduce performance of a task that has already been learned, but it can also interfere with learning from producers in the first place. When pigeons learned to remove a stopper from an inverted test tube, causing grain to fall out (Figure 13.3; Giraldeau and Lefebvre 1987), eight out of eight observers that watched another pigeon remove the stopper and eat the grain did the same themselves when given the opportunity. If the observers could scrounge some of the demonstrator's grain, however, only two out of eight birds learned in the same number of trials. Just as with paper piercing, when a trained observer was introduced into a laboratory flock, a few birds learned the tube-opening task and became consistent producers, whereas the majority scrounged as long as the producers were present. Taken together, these observations indicate that scrounging influences learning, perhaps because pigeons cannot divide attention between looking for food to scrounge and watching what a demonstrator is doing. Some other species of birds, however, may be able to scrounge and learn at the same time (Lefebvre and Bouchard 2003).

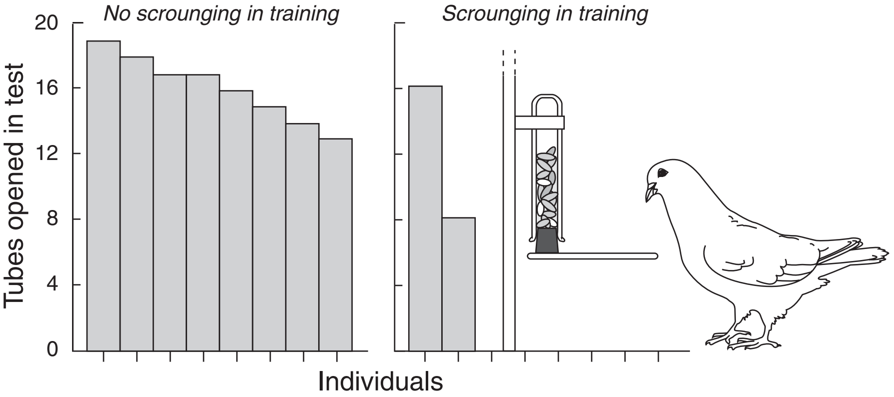


Figure 13.3. Apparatus and results in experiments demonstrating effect of the opportunity to scrounge from the demonstrator on social transmission of a food-finding skill. Data for eight individuals per group, each given 20 opportunities to open a test tube in the test phase. Data redrawn from Giraldeau and Lefebvre (1987) with permission.

13.1.3 Public information, cues, and signals

A young rat approaching a food site frequented by other rats is already familiar with the flavors of some safe foods. This is *private information.* In contrast, the rat excrement and odors of other rats around the site constitute *public information* that quantities of edible food are present, and indeed these cues attract rats (Laland and Plotkin 1993). Similarly, by trial and error a Montreal street pigeon might acquire private information about how to open one of Giraldeau and Lefebvre's feeders, but to find a good foraging patch it could use public information like the sight of a flock of pigeons feeding.

At the end of the twentieth century, uses of public versus private information became a lively topic in behavioral ecology (Danchin et al. 2004; Valone 2007), in parallel with interest in eavesdropping in animal communication (Chapter 12). When animals respond to the behavior of other animals or a byproduct of it to find food or other resources, they are said to be using public information. Using public information does not necessarily require or result in social learning of any kind, but it might. For instance, the young rat feeding in the presence of other rats or their excrement becomes familiar with the flavor of whatever it is eating there. *Eavesdropping* is reserved for cases in which the public information consists of communicative signals, but from a mechanistic point of view there is not necessarily any distinction (Bonnie and Earley 2007; Valone 2007). And like other kinds of public information, signals may arouse specific behaviors or affective states in eavesdroppers without anything necessarily being learned. For example, seeing conspecifics fighting raises testosterone levels in cichlid fish (Oliveira et al. 2001).

In Section 13.2 we analyze how learning from public information might take place. Here a series of studies with stickleback fish will illustrate some potentially cognitively interesting questions about how public and private information interact. In all of them, the fish acquired information about the value of feeding patches in a setup like that illustrated in Figure 13.4. An observer fish confined to a central compartment could see fish feeding in each end of a tank. It could not see the worms that were being delivered on different schedules in the two patches, but it could see the demonstrators feeding and attempting to feed. Both nine-spined and three-spined sticklebacks used public information, in that shortly after demonstrations they chose a patch where fish had been feeding over one where no food had been delivered. However, when both patches had had food, only the nine-spined species chose the one that had delivered food at the higher rate (Coolen et al. 2003; see also Webster and Hart 2006).

Public and private information were opposed in a further study with nine-spined sticklebacks by first letting observers learn for themselves that the richer of two patches was always at a given end of the tank. Between 1 and 7 days later they were exposed to conflicting public information (demonstrators feeding more frequently at the observer's formerly poor patch than at the rich one) and immediately tested. Fish whose private information training had ended the day before behaved as if ignoring the public information, whereas those trained a week before strongly preferred the patch that had just been seen to be better (Fig 13.4). Fish tested at intermediate delays showed no preference (Experiment 2 in van Bergen, Coolen, and Laland 2004). The authors concluded that the fish "will weight public and private information appropriately depending on circumstances." This implies that fish tested at the longest delay still remembered what they learned individually a week before but were reweighting this information. However, because the experiment did not include

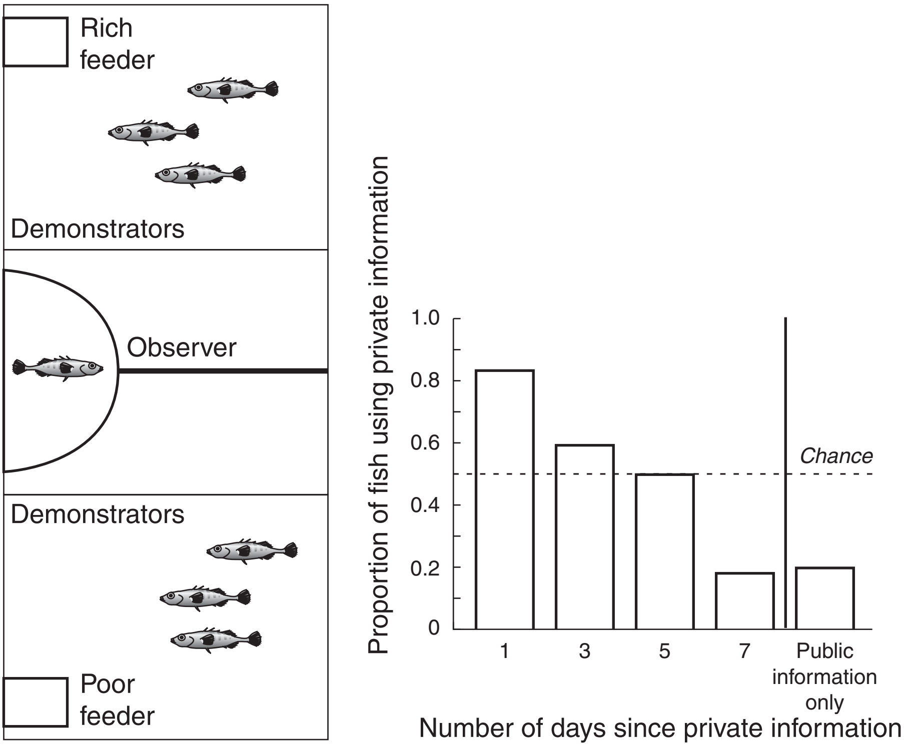


Figure 13.4. Setup in which an observer stickleback acquires public information about two food patches by watching others feed there immediately before it is allowed to choose between the patches. In the observer's own past experience (private information) rich and poor feeders were swapped. Hence, "using private information" means choosing the currently poor feeder. After van Bergen, Coolen, and Laland (2004) with permission.

control fish not exposed to conflicting public information just before testing, the results could as well reflect forgetting of the original private information.

Of course the findings can still be described functionally as showing that recent information is treated as more reliable, but the absence of a forgetting control illustrates how a focus on a functional account can overlook interesting and even important mechanistic questions. (Which is not to say that a focus on mechanism cannot be similarly narrow.) Similarly, the contrast between public information and "social cues" in this context (Coolen et al. 2003) is perhaps not meaningful mechanistically if the former refers to the feeding rate of demonstrators and the latter to their numbers. There seems to be little other than precedent to justify such distinctions among sources of social information (Bonnie and Earley 2007; Valone 2007) nor much reason to think they affect behavior through fundamentally different mechanisms. Indeed, once an animal has learned the value of a site, it may not retain any information about whether it learned from seeing conspecifics there or being there itself.

13.1.4 Copying others' choice of mate

If females are actively choosing mates, some males will be popular simply because they have more of whatever females are basing their choices on: more intense colors, more complex songs, or whatever. But if assessing a potential mate's characteristics takes time, entails a risk of predation, or is otherwise costly, females could reduce their assessment costs by choosing males they see other females choosing (Dugatkin 1996; White 2004). Of course functional copying would result from females using cues that a male has been chosen before, such as the presence of eggs in species where males guard a nest. But remembering the identity of males chosen by other females and later preferring those males would be an example of social learning comparable to that involved when client fish learn about good cleaners or fighting fish and songbirds learn about winners and losers by eavesdropping on their fights (Chapter 12). Indeed, the first examples of mate choice copying involved fish, guppies (review in Dugatkin 1996), but although other fish show mate copying, this example has proven difficult to replicate, perhaps because in guppies mate copying is confined to certain populations (Galef and Laland 2005).

In birds, female black grouse visiting a lek (a communal mating ground) apparently prefer males seen copulating. Stuffed females were placed in males' territories, either on the ground where males could mount and copulate, or on sticks as if sitting in a bush, where males could not copulate. Subject females spent more time in the former than in the latter territories (Hoglund et al. 1995). Both females and males of another bird species, Japanese quail, have been the subjects of perhaps the most extensive investigation of mate copying in any species (White 2004). In the basic demonstration of this phenomenon, a female is first confined equidistant from two males, one of whom is courting a female while the other is alone (Figure 13.5). Later—usually immediately afterward—the subject female is released and the time she spends in defined areas near each male is recorded. "Mate choice" here consists of spending more time near one male than the other, but this measure does predict partner choice when the birds are free to interact.

Clearly there are a number of potential confounds in this simple test. For example, the female might be choosing a male that had been seen courting or a male that had courted recently or the place where such events had occurred. It turns out that what matters is not seeing mating per se but seeing a female near the male (see White 2004). Given that male quail are quite aggressive, a close approach by a female is enough to indicate that a male is willing to mate. Male quail also learn which members of the opposite sex have been chosen by others, but experiments analogous to those with female quail subjects show they prefer a female that has *not* been courted by another male. This sex difference in behavior resulting from essentially similar learning (i.e., in performance rules) means that males do not invest in courting females that are already inseminated.

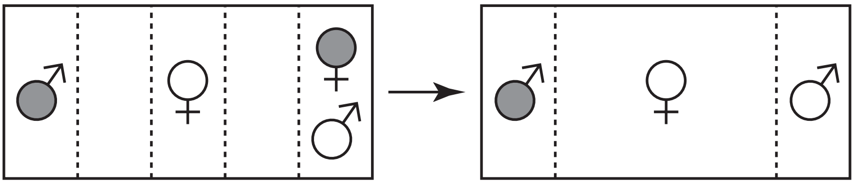


Figure 13.5. Setup for tests of mate choice copying by female quail or other animals. Dashed lines represent transparent barriers.

13.2 Mechanisms: Social learning without imitation

13.2.1 Another example and some distinctions

Not so long ago, milk was delivered to the doorsteps of homes in Great Britain and elsewhere in glass bottles sealed with foil or paper. The milk was not homogenized, so it had a thick layer of cream at the top. In the 1920s and 1930s blue tits began puncturing the bottle tops and stealing the cream (Figure 13.6). Milk bottle opening became relatively common in a few isolated areas, suggesting that it was being transmitted socially within them (Fisher and Hinde 1949; Hinde and Fisher 1951; Lefebvre 1995a). Pecking or tearing open a bottle top is clearly not imitation, since pecking and tearing at bark and seeds are prominent components of tits' foraging behavior, but the birds could have learned from one another where to direct these behaviors. This learning need not have been inherently social, however. Rather, the products of one individual's behavior—opened bottles—could have provided the conditions under which another individual learned for itself. The naive tit drinking from an already-opened bottle would associate bottles with food and then approach closed bottles and engage in food-related behaviors like pecking and tearing, which would be reinforced (Hinde and Fisher 1951).

Sherry and Galef (1984, 1990) showed that indeed milk-bottle opening can develop through this process. They taught captive black-capped chickadees, a North American tit species, to open small cream tubs like those served in restaurants. Then some experimentally naive chickadees watched demonstrators opening cream tubs while chickadees in another group simply learned to feed from opened tubs. Birds in both groups were subsequently more likely to open sealed tubs on their own than chickadees that had observed an empty cage containing a closed cream tub, but the proportion of opening individuals in the two groups did not differ.

The products of a conspecific's behavior may facilitate learning by naive individuals in a number of ways. Adult black rats of the Israeli pine forests, described at the beginning of the chapter, do not directly teach or demonstrate efficient pine cone stripping to their young. Rather, cones partially stripped by experienced rats have their scales exposed in such a way that a young rat gnawing at the cone can easily remove them in an efficient, spiral, pattern, and get at the seeds underneath. Naive rats encountering completely unopened cones gnaw them all over in an inefficient way

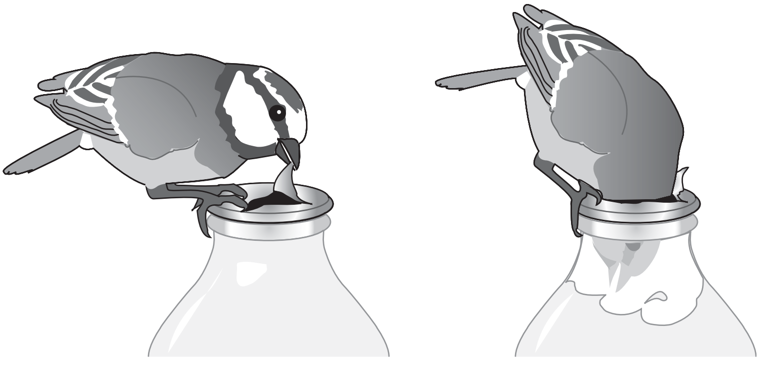


Figure 13.6. A blue tit peeling the top off a milk bottle and drinking the cream underneath. Redrawn from Gould and Gould (1994) with permission.

(Aisner and Terkel 1992; Zohar and Terkel 1996). Thus efficient stripping of scales from pine cones, which the rats must develop in order to access their only food in the forest, is socially transmitted when the young rats follow adults around, steal partially opened cones, and continue the stripping themselves (Terkel 1995). This is "social learning" only because the adults create the conditions necessary for it to occur; successful actions emerge through trial and error learning by individuals. In other cases, the products of one individual's behavior attract others to the same sites, allowing those individuals to learn something there. For instance, rats' preference for sites surrounded with fresh rat excrement leads them to become familiar with food eaten by other rats (Laland and Plotkin 1991). This kind of social influence is referred to as *local enhancement* or *stimulus enhancement* (Box 13.1; Galef 1988; Whiten and Ham 1992; Heyes 1994a). The demonstrator's behavior or some product of it attracts the observer to a location or stimulus which it then learns about on its own.

13.2.2 Observational conditioning

In observational conditioning the demonstrator's actions or the affective state and behavior they arouse in the observer are associated with stimuli present at the time. As a result, the observer performs similar species-typical behavior when it encounters those stimuli again by itself. One striking example is provided by the mobbing that small birds direct toward predators. In mobbing, as the name suggests, birds approach a predator in a group, calling in a distinctive way. This behavior functions to alert potential victims in the area to the location of the predator and may also drive the predator away. Some common predators like owls may be mobbed even by naive birds, but mobbing can depend on social learning (Curio 1988). Social transmission of enemy recognition has been studied in European blackbirds in the apparatus depicted in Figure 13.7. A "teacher" sees a stuffed owl in the central compartment. The "pupil" sees and hears the teacher mobbing the owl and is stimulated to engage in mobbing behavior itself. However, in its side of the central compartment the pupil sees not the owl but a harmless bird like a honeyeater or an owl-sized plastic bottle. When the pupil later encounters the training object by itself, it will mob it. The pupil can now "teach" naive blackbirds to mob bottles or honeyeaters. Such mobbing can be socially transmitted across chains of up to six birds (Curio, Ernst, and Vieth 1978).

This is a straightforward case of Pavlovian conditioning. Because the mobbing demonstrator elicits mobbing by the pupil, the pupil acquires an association between the bottle or honeyeater and its own mobbing behavior system (Figure 13.8). Nonassociative controls are necessary to be sure that mobbing is indeed associated specifically with the training object. For example, birds that have mobbed the honeyeater should not mob bottles as strongly, and vice versa (for review see Curio 1988; A. Griffin 2004). Experiments on acquired mobbing have generally begun with a phase in which the subjects are habituated to the bottle or the honeyeater, so later mobbing is clearly the result of having seen the teacher mob. Robust learning to such objects after habituation to them suggests that latent inhibition is not very strong in this system; naive individuals can thus learn about predators even after encountering them while alone. Another possibly specialized feature of this system is that a more predator-like object, a stuffed honeyeater, supports stronger acquired mobbing than a bottle (Curio 1988). Meerkats, monkeys, and some other social mammals also mob predators, but how mobbing develops in these species has not been studied to the same extent as in birds (A. Griffin 2004; Graw and Manser 2007).

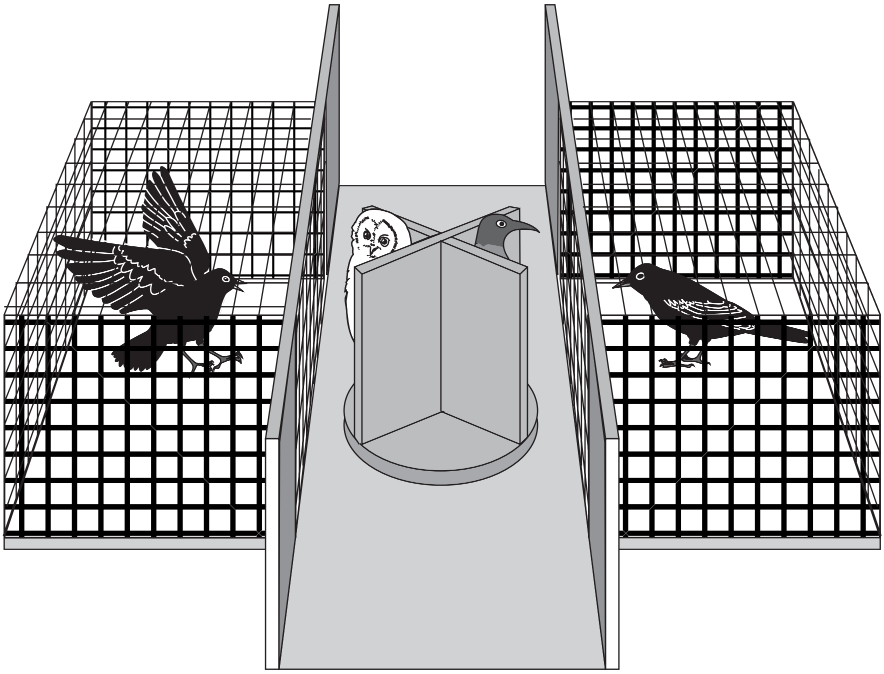


Figure 13.7. Setup for the experiments of Curio and his colleagues in which one blackbird (the one on the left) can "teach" another to mob a harmless object, here a model honeyeater. Redrawn from Gould and Gould (1994) with permission.

Social transmission of predator recognition makes functional sense because individuals that must experience predators for themselves to learn they are dangerous may not survive those experiences. The best-analyzed example involves monkeys' fear of snakes (Mineka and Cook 1988). Monkeys reared in captivity do not exhibit fear the first time they encounter live or toy snakes. If they watch another monkey behaving fearfully toward a snake, they later do the same themselves. As with mobbing, during the learning trial the naive observer exhibits behavior like the model's (in this case responses such as withdrawal, vocalization, and piloerection). If naive monkeys observe a model behaving fearfully toward a snake and neutrally toward another object like a flower, they acquire the same discrimination. For example, if they are later offered raisins that are out of reach beyond a flower or a snake, they reach quickly over the flower but refuse to reach over the snake.

Selective acquisition of fear shows that the animals are not simply sensitized to behave fearfully to any and all relatively novel objects in the experimental situation. However, even though naive monkeys do not show fear to snakes or flowers, they acquire fear much more quickly to snakes than to flowers (Cook and Mineka 1990). Subject monkeys that saw videotapes of demonstrators apparently reacting fearfully to snakes and nonfearfully to flowers acquired fear of snakes, just as if they had seen live demonstrators. However, subjects exposed to tapes edited to depict a monkey fearing flowers but not snakes did not learn to fear either stimulus. This comparison shows simultaneously that snake fear is acquired associatively (it depends on the specific pairing of demonstrator's behavior with a snake) and that the associative process is selective (not any initially neutral object will be feared). Selective learning

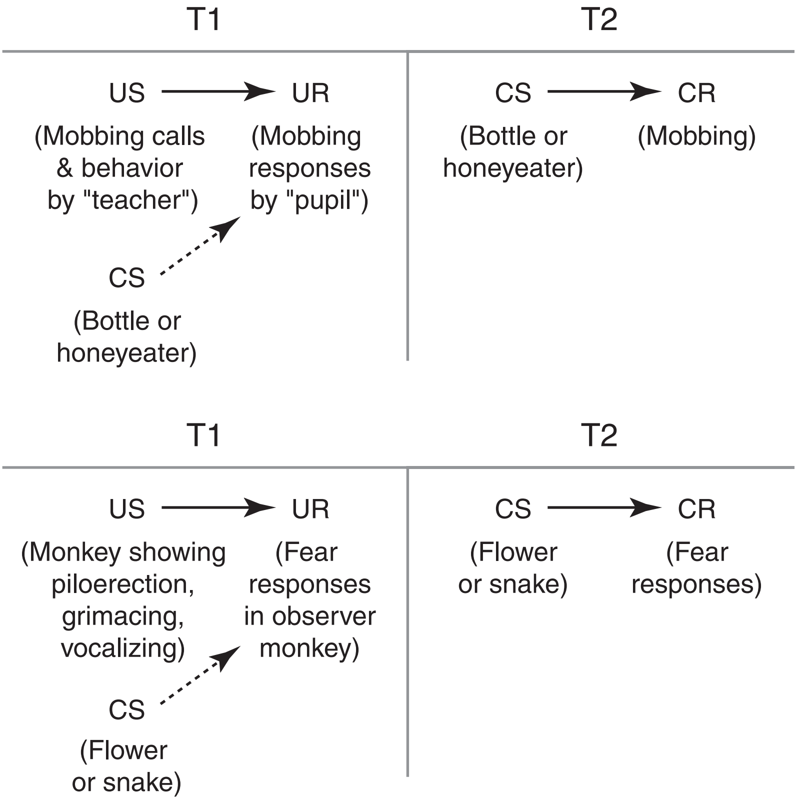


Figure 13.8. Observational conditioning of mobbing or fear as classical conditioning.

about snakes seems to be specific to fear. Monkeys trained with video images of either snakes or flowers paired with food learned equally quickly in both conditions (Cook and Mineka 1990, Experiment 3). However, the stimuli used and the discriminations to be learned were not exactly the same in this experiment as in those involving socially transmitted fear, so this conclusion must be somewhat tentative (Heyes 1994a).

Social learning about aversive events seems to be phylogenetically fairly general (see A. Griffin 2004), as functional considerations suggest it should be. At the same time, the events learned about are species-specific. Several species of birds learn to avoid aversive foods by watching others (Mason 1988; but see Avery 1994). Curio's paradigm (Figure 13.7) has been used to train New Zealand robins to recognize stoats, an introduced predator (Maloney and McLean 1995). Similar training has been used to prepare captive-raised young of endangered species for release in the wild (A. Griffin 2004). Suboski (1990) termed the form of learning here *releaser-induced recognition learning* because in ethological terminology a sign stimulus present at T1 elicits behavior via an innate releasing mechanism. At T2 the animal reveals its recognition of a neutral stimulus that accompanied the releaser. However because the interevent relationships necessary for learning seem to be the same as in simultaneous Pavlovian conditioning (Figure 13.8), it is not clear that any term other than *observational conditioning* (Heyes 1994a) is needed.

Observational conditioning is not confined to aversive USs. Young chicks peck at items they see another chicken or even a motor-driven model beak pecking at, behavior that would normally direct them to food being eaten by a mother hen. If a young chick watches a beak-like object selectively "pecking" dots of one color on the other side of a barrier, it pecks at that same color on its side and retains this discrimination when later tested alone (Suboski and Bartashunas 1984). Similarly, when young junglefowl watch others pecking for food in a distinctively decorated bowl they later peck more in bowls decorated in the same way (McQuoid and Galef 1992). This socially acquired preference was weak and transitory if the bowls were empty in the test, but it was robust and long-lasting if the birds got food in the test. This might be typical of socially acquired preferences (Galef 1995). Because positive reinforcement can perpetuate the behavior once the animal makes the socially induced choice, social learning about positive stimuli need have only a small initial effect to have important consequences.

Most examples of social learning described earlier in this chapter could be described as observational conditioning. The social experiences that influence choice of mates, food patches, flavors, or opponents in a fight are in fact simultaneous pairings of particular individuals, places, or other cues with motivationally significant stimuli. However, an associative account has implications that need to be tested. At the most basic level, what is the role of contingency between the putative CS and US? Contingency apparently plays a role in socially influenced patch choice in nine-spined (but not three-spined) sticklebacks in that out of two patches where they had seen other fish feeding they preferred the one where food deliveries had been more frequent (Coolen et al. 2003). Cue competition effects might be expected, too, but overshadowing and blocking failed to appear in a study of socially transmitted food preferences in rats (Galef and Durlach 1993). In socially learned mate choice, female zebra finches learn about both a male's identity and an artificial ornament, the color of the band on a male's leg (Swaddle et al. 2005), but whether these cues compete for learning was not tested, for example by manipulating their relative validity. In candidate examples of observational conditioning other than mobbing and snake fear it is unclear how the demonstrators' behavior acts as a US. However, progress in identifying the effective US has been made not only with rats' flavor preferences, but also with mate choice in quail (Ko?ksal and Domjan 1998; White 2004), feeding techniques in pigeons (Palameta and Lefebvre 1985), and feeding patch choice in sticklebacks (Coolen et al. 2005).

In summary, there is plenty of scope for more detailed analyses of what and how animals learn from observing conspecifics engaged in species-typical behavior. In the past such research has been discouraged by confusion over terminology and a tendency to dismiss aspects of social transmission other than imitation as both uninteresting and well understood. As a result there are few such phenomena for which the conditions for learning, the content of learning, and/or the effects of learning on behavior have been clearly delineated. Typical of terms in social learning, and notwithstanding attempts at clarification by Heyes (1994a) and others, *observational conditioning* continues to refer to a confusingly large number of phenomena (cf. Hoppitt et al. 2008). Some of them seem to involve a special learning mechanism, others do not. Learning from watching another animal perform an arbitrary behavior B and receive outcome O could be described as S-S (stimulus-stimulus) learning. It might even follow associative principles, but no performance rule for normal conditioning seems able to explain how knowledge that someone else gets O for performing B leads the observer to perform B when it desires O (Papineau and Heyes 2006).

13.2.3 Species differences

Social learning might be expected to vary across species with the conditions of social life. So far, however, we have encountered no evidence for any qualitatively special *kind* of representations or computations. Socially transmitted behavior such as black rats' pine cone stripping and tits' milk bottle opening is best described as *socially influenced learning* in that conspecifics provide the conditions under which the given behaviors are learned by normal associative means. And mate choice copying, socially transmitted food and patch preferences, or enemy recognition all seem to be instances of observational conditioning, as broadly defined. But smelling food together with carbon disulphide or seeing a hen pecking red food results in learning only in species with the appropriate specializations of perception, attention, or motivation. Rats' breath is presumably not interesting to chickens, nor is the sight of chickens pecking interesting to rats. Specializations of learning per se could also play a role, as illustrated by the predisposition of monkeys to acquire fear to snakes but not flowers, stimuli which are apparently equally easy to associate with food (Mineka and Cook 1988). However, with the exception of demonstrations that learning about sexual partners is expressed through different performance rules in male versus female quail (White 2004), there are virtually no thorough comparative studies of any of the sorts of social learning reviewed in this section. But there are a few tantalizing suggestions.

For example, the notion that animals which do not spend much time in family groups should not learn very well from adults was tested by exposing young brush turkey chicks to a brush turkey robot pecking at corn in a red as opposed to a blue dish (Go?th and Evans 2005). In studies like those already mentioned in this section (see Go?th and Evans 2005), young chickens acquire the same discrimination as a model. However, brush turkeys bury their eggs in a mound of rotting vegetation. The young hatch without adults around and have little opportunity for social learning about food. Indeed the young brush turkeys in Goth and Evans's experiment did not prefer the color pecked by the model when tested the next day even though they had approached that color more during the demonstration. Of course data from a single set of conditions are seldom enough to infer a species difference, let alone show what it consists of, but the effect is quite robust in the comparison species, junglefowl and their domestic descendents. The young brush turkeys seem to attend to and copy the choice of the robot so perhaps they forget more quickly than chickens do.

One possible source of species differences in social learning is attentiveness to the activities of other animals, which could perhaps be acquired. Such differences in attention could be responsible for the differences in social learning about the locations of food caches among corvids described in Chapter 8. Indeed, there is some indication of differences in social attention in two other corvids, ravens and jackdaws. This was demonstrated with the setup shown in Figure 13.9 (Scheid, Range, and Bugnyar 2007), one adopted from experiments with primates (e.g., Range and Huber 2007). Both ravens and jackdaws are quite social, but the nature of their sociality differs in a way that the authors argue favors ravens paying more attention to the activities of others, especially their feeding. As predicted, raven subjects spent more time observing a conspecific than did jackdaws. Again, this is only a single set of conditions, and it is important to know whether the results hold up when conditions such as size and ease of access to the viewing ports are varied. Still, this seems a promising method for measuring social attention.

Possible specializations for social learning can be tested very elegantly if the relevant task can be acquired under both social and nonsocial conditions, as in studies

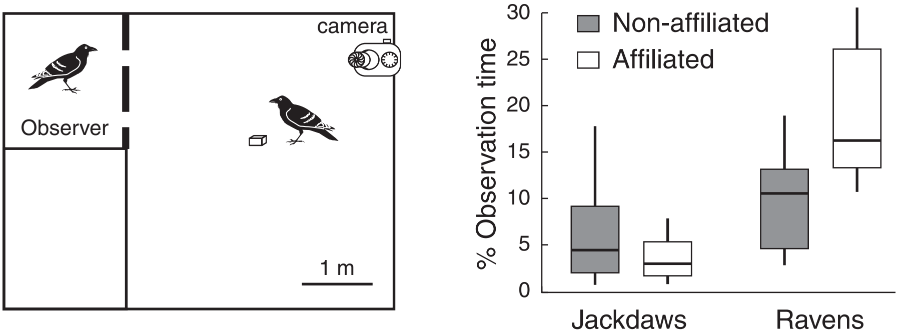


Figure 13.9. Setup for measuring social attention, as used with ravens and jackdaws. Data consist of the proportion of time the camera detected the observer in front of the viewing ports, watching the activities of a feeding conspecific with which it was closely affiliated or not. Adapted from Scheid, Range, and Bugnyar (2007) with permission.

of feeding skills in social versus nonsocial birds by Lefebvre and his colleagues (Lefebvre and Giraldeau 1996). They tested the notion that opportunistic animals such as rats and pigeons, which have fairly generalized food requirements and can take advantage of a wide range of niches, might be more prone to social influences than more conservative species. But because opportunism by definition is the ability to function effectively in a many different environments, opportunistic animals might have generally enhanced learning ability. On this latter hypothesis performance on social learning tasks should correlate positively with performance on nonsocial tasks. Yet another hypothesis is that social learning is most evident in species whose foraging is a matter of *scramble competition,* that is, many individuals feeding at once on limited food sources, as opposed to *interference competition,* where foragers aggressively exclude competitors. Success in scramble competition is a matter of speed, so slow individuals can benefit by learning the techniques being used by their speedier competitors (Lefebvre and Giraldeau 1996). If all these factors are important, then social, opportunistic animals that encounter scramble competitions for food will be the best social learners, whereas solitary species that compete with others by exclusion and have conservative food habits will be the poorest.

All these predictions were addressed by comparing how pigeons and a close relative, the Zenaida dove (*Zenaida aurita*) from Barbados, learn various foraging tasks socially and individually. Pigeons are social and opportunistic and encounter scramble competitions while foraging, so they should excel at social learning. Most Zenaida doves are territorial year-round but tolerate and even forage with birds of other species like grackles (*Quiscalus lugubris*). At first glance, Zenaida doves and pigeons differ in social learning just as the three ecological hypotheses predict. Naive pigeons and doves were equally unlikely to push the lid off a bowl of grain (Figure 13.10, top row), but after watching a conspecific push off the lid and eat the grain underneath, more pigeons than doves pushed off the lid by themselves (Lefebvre, Palameta, and Hatch 1996). However, the pigeons were also quicker to feed from an open bowl of food in the experimental situation, and pigeons pushed off the lid sooner than doves after simply eating from the bowl with no demonstrator present (Figure 13.10, middle row).

These findings suggest that pigeons and Zenaida doves differ not in social learning ability but in some general learning ability or in responses to contextual variables (see Chapter 2). However, the story is still more complicated: Zenaida doves'

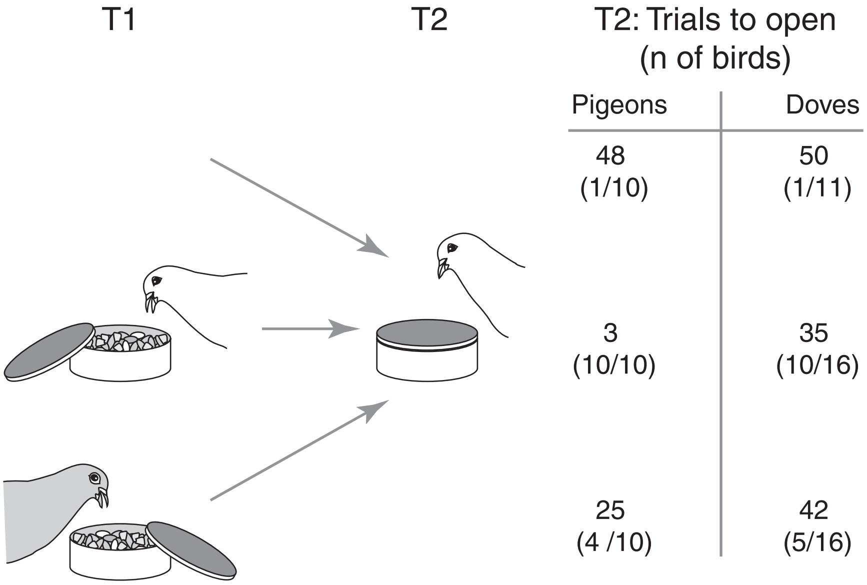


Figure 13.10. Design and results of experiment by Lefebvre, Palameta, and Hatch (1996) comparing social and individual learning in feral pigeons and Zenaida doves. Each bird had 50 opportunities to open the lid in the test; birds that never opened it were given a score of 50. Numbers in parentheses are the number of birds ever opening the bowl as a fraction of the number of birds in the group.

susceptibility to social influence depends on the species of tutor and on the social situation in which they have been living. In two different feeding tasks, territorial Zenaida doves copied grackles rather than other doves whereas subjects from a gregarious population of Zenaida doves learned more quickly from a dove than from a grackle. These population differences may reflect differences in experience. Gregarious doves could also be shaped more readily than territorial doves to perform a complex food-finding task, suggesting the populations differ in learning ability generally or in something else that influences speed of learning such as neophobia (Dolman, Templeton, and Lefebvre 1996; Carlier and Lefebvre 1997). More extensive comparisons of pigeons and doves, as well as data on several tit species, show that performance on social learning tasks is positively correlated with performance on comparable nonsocial tasks (Lefebvre and Giraldeau 1996). It is also correlated with innovation, both across species and in comparisons of individuals within one species, pigeons (Bouchard, Goodyer, and Lefebvre 2007). Just as innovativeness reflects a concatenation of more general cognitive abilities (Box 2.2) so may "social learning," at least when measured as successfully copying others' behavior in naturalistic conditions. But this analysis begs the question we take up next: whether the narrow but important kind of social learning known as imitation (Box 13.1) is a specialized kind of learning shown by only a few species.

13.3 Mechanisms: Imitation

In imitation, the *form* of a behavior is learned from a demonstrator. Interest in imitation has a long history (cf. Whiten and Ham 1992), but only toward the end of the twentieth century was much progress made in understanding it, as researchers began looking at the development and mechanisms of imitation in humans. As a result candidates for imitation in other species were no longer simply compared to some assumed ideal of human imitation but children and apes were compared directly, often in the same experiments with tasks resembling those chimpanzees are thought to learn socially in the wild. In addition, the discovery of mirror neurons in monkey brains in the late 1990s provided a possible neural mechanism for imitative behavior. All these new findings in turn stimulated new theories about how imitation is possible and its role in the evolution of human culture.

13.3.1 Some history

Imitation is one of the mental faculties Darwin (1871) claimed other species share with humans. Anecdotes about domestic animals apparently imitating complex actions performed by people featured prominently in the evidence for mental continuity collected by Romanes and others. Many of these anecdotes involved cats and dogs learning to open doors and gates by manipulating latches, handles, and door knobs. One of the more colorful of these featured a cat belonging to Romanes's coachman.

> Walking up to the door with a most matter-of-course kind of air, she used to spring at the half-hoop handle just below the thumb-latch. Holding on to the bottom of this half-hoop with one fore-paw, she then raised the other to the thumb-piece, and while depressing the latter, finally with her hind legs scratched and pushed the doorposts so as to open the door. . . . Of course in all such cases the cats must have previously observed that the doors are opened by persons placing their hands upon the handles, and, having observed this, the animals forthwith act by what may be strictly termed rational imitation. . . . First the animal must have observed that the door is opened by the hand grasping the handle and moving the latch. Next she must reason, by 'the logic of feelings'—If a hand can do it, why not a paw? (Romanes 1892, 421–422).

"If a hand, why not a paw" captures very well what is cognitively distinctive about imitation. True imitation entails using a representation of a demonstrator's action to generate an otherwise unlikely action that matches the demonstrator's. The cat at the gate is at most matching visually perceptible actions of its own to equally perceptible actions of another, that is, grasping the latch, and so forth. An apparently greater cognitive challenge is reproducing a model's *perceptually opaque* actions, that is, those like facial expressions or whole-body movements that one cannot see or hear oneself perform (Heyes and Ray 2000). In either case, performance of a species-specific activity under the direct influence of another animal does not qualify. Thorndike (1911/1970) made this point with an anecdote about a flock of sheep being driven along a path, each jumping where the one in front of it had jumped, even when the barrier that originally occasioned jumping had been removed. "The sheep jumps when he sees other sheep jump, not because of a general ability to do what he sees done, but because he is furnished with the instinct to jump at such a sight, or because his experience of following the flock over boulders has got him into the habit of jumping at the spot where he sees one ahead of him jump."

What Thorndike emphasized still bears repeating (Galef 1996a): by themselves, observations like those of cats opening latches or sheep all jumping in the same place cannot reveal how such behavior came about. Field data can be enormously suggestive, but experiments, or at least systematic observations of acquisition, are required

Box 13.2 Vocal Imitation: Bird Song Learning

Song learning by birds is the best-studied and most widely distributed example of learning by imitation, yet is it usually omitted from theoretical discussions of animal imitation, largely because the actions copied are not perceptually opaque. That is, the learner hears itself as it hears others. In addition because it is found in only one group of species and involves a system highly specialized both behaviorally and neurally it may seem to have few lessons to teach about imitation in general. But by the same token it is important in the context of this book as an excellent example of a specialized module fine-tuned in species-specific ways.

Song refers to birds' species-typical musical vocalizations, usually emitted primarily by males in the breeding season. Depending on species, males sing from one to over a hundred distinct songs. Song functions in territory defense and advertisement and in attracting mates. Females, of course, must respond selectively to the features of song identifying males of their species, and experience can have a role here too. Vocal learners have been found in oscine birds (a suborder of passeriformes or perching birds, 46% of the approximately 9000 species of birds; Gill 1995), parrots, and hummingbirds. Many are altricial, that is, they hatch naked and helpless, but may develop very rapidly and leave the nest within two or three weeks. In temperate climates, home of most best-studied species, hatching takes place in spring or early summer, when adult males are still singing. Breeding, and hence singing by adults, ends by late summer. Many species migrate for the winter and return to the breeding grounds the next spring, when the young males are ready to breed. This life history means that song learning has two phases, a sensory phase, in which the bird stores auditory information, and a motor phase perhaps many months later, in which this memory guides the bird's song. The onset of the motor learning phase may be evident in *subsong,* quiet, rather formless vocalizations with few identifiable elements of adult song. Shortly before full song appears is a period of plastic song. Plastic song includes many elements identifiable in adult song, but these may drop out as the bird comes to sing one or more (depending on species) crystallized adult songs that may remain in its repertoire for life (Catchpole and Slater 1995). Some species have a third, action-based learning phase, when feedback from other birds influences the male's repertoire.

Contemporary research on the behavioral and neurobiological aspects of bird song learning is the subject of books in itself (e.g., Marler and Slabbekoorn 2004; Zeigler and Marler 2004), but its major themes are evident in research on one of the first species studied in detail, the white-crowned sparrow of North America (*Zonotrichia leucophrys*). Each male white-crowned sparrow has a single, rather simple, song, which he shares with his neighbors. Males in different geographical areas have different songs, that is, there are local dialects (Marler and Tamura 1964). White-crowned sparrows reared in isolation sing abnormal songs, but their songs still develop, from disorganized and variable vocalizations to a single stereotyped song with some species-typical characteristics. Deafened birds also fail to develop normal song, but their vocalizations are more abnormal. The contrast between isolated and early-deafened birds (Figure B13.2a) indicates that progression from subsong to crystallized but atypical song in isolates depends on auditory feedback from the bird's own vocalizations. Feedback may not be important for maintaining the structure of crystallized song, as indicated by the fact that white-crowned sparrows with normal early experience that are deafened as adults continue to sing normally.

White-crowned sparrows taken from the nest at a few days of age and reared in isolation acquire normal song if they hear tape-recorded white-crowned sparrow songs between 10 and 50 days of age (Marler 1970). They acquire the song they hear even if it is not from the same dialect area where they were born, but they do not learn the songs of other species from tape recordings. Just as with imprinting (Chapter 5), the sensitive phase for learning may depend on the stimuli available for learning. For example, white-crowned sparrows learn from live tutors when tapes are no longer effective. They will also learn the songs of other species from live tutors.

The model of song learning suggested by these observations is depicted in Figure B13.2b (Konishi 1965). The bird hatches with a rough representation of its species-typical song, an *auditory template.* During the sensitive period for sensory learning, the template selects in a species-specific way what songs will be learned (see also Section 1.2.2 and Figure 1.3). The hypothetical template is separate from general auditory selectivity: birds can perceive and memorize many songs that they never sing themselves, as in recognizing their neighbors. Early experience hearing song is stored as modifications of the template. During the motor learning phase the bird learns to sing songs he has heard by matching his vocalizations to the refined template. A bird reared in isolation has only the rough, unmodified, template as a guide during the motor phase of learning, as witnessed by the fact that its song has more species-typical characteristics than the song of a bird deafened before the onset of singing.

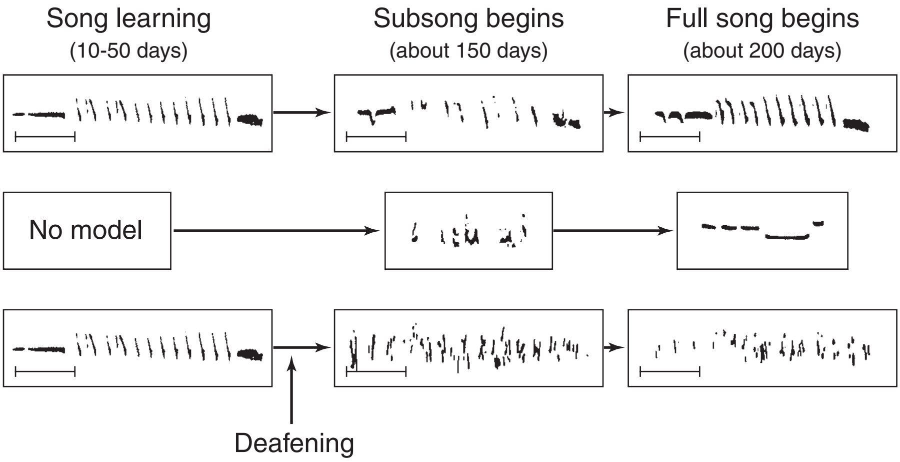


Figure B13.2a. Comparison of song development in normal and isolated male white-crowned sparrows (top two rows) and in birds deafened after hearing normal song during the sensitive period for vocal learning. Left-most sonagrams (plots of sound frequency vs. time) in top and bottom sequences represent the songs heard by the subjects; others represent the songs they sang. After Marler (1976) with permission.

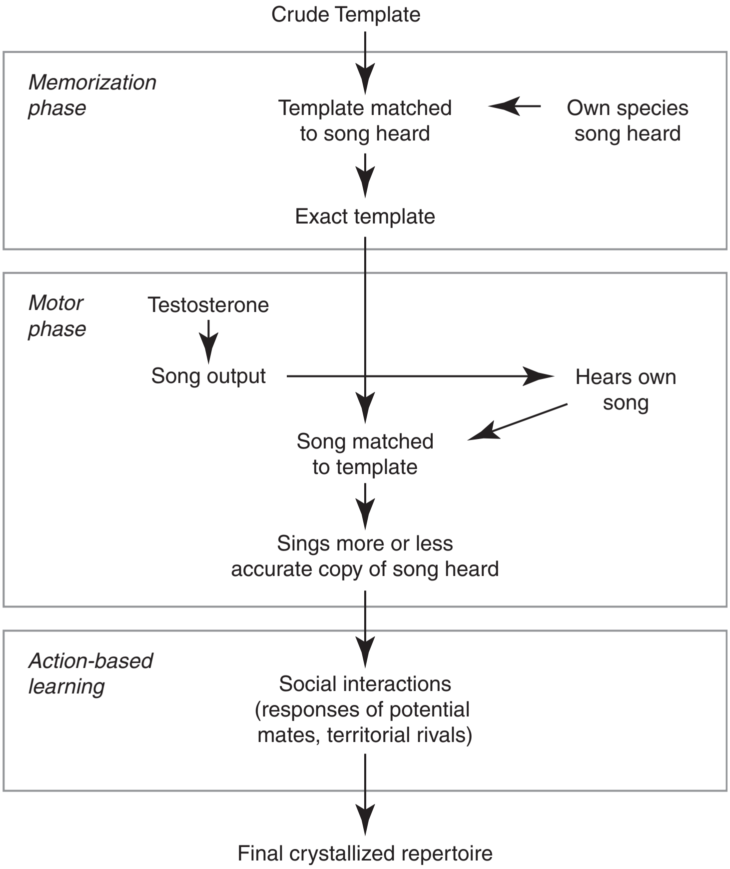


Figure B13.2b. The template model of bird song learning. After Slater (1983) with permission.

Species differences in song learning can be described within the framework provided by the template model. The optimal time and stimuli for learning vary across species in ways related to the species ecology (Beecher and Brenowitz 2005), as do the roles of early learning and later experiences. Purely acoustic features may be used to select what is learned, as in swamp and song sparrows (see Figure 1.3), or features of the singer may be important, for example learning may be best from the father or a socially dominant male. Some species, such as starlings, mimic songs of other birds and all sorts of natural sounds, that is, they show very little species-specific selectivity. And song production may not require learning early in life. In the brood-parasitic cowbirds, which are raised by adults of another species, young males sing effective cowbird song but its form is later shaped by the aggressive responses of other males and the sexual responses of females, essentially through operant conditioning (West and King 1988).

Species that learn song have a specialized network of interconnected nuclei, *the song system,* that is involved in song perception, learning, and production, although other parts of the brain may be involved as well (for a brief review see Bolhuis and Gahr 2006). The neurobiological basis of bird song is very well characterized yet a continuing source of new insights. For example, techniques for recording activity of single cells during singing have revealed the equivalent of mirror neurons, cells that fire preferentially to note patterns in the bird's own song when sung by itself or another bird (Prather et al. 2008). Singing has been studied as an example of a highly practiced and precise motor skill that nevertheless shows instructive forms of plasticity (Turner and Brainard 2007). And over the years discoveries about the song system have had wider implications. Seasonal neurogenesis in adult brains, presumably related to the seasonality of singing in some way, was demonstrated in the song system and stimulated a search for neurogenesis in other systems. And like the neurobiological basis of human language, the song system is lateralized and is most plastic early in life.

to know whether behavior has developed through imitation or in some other way. Thorndike's (1911/1970) own experiments were based fairly directly on Romanes's stories about dogs and cats opening latches. But instead of letting animals open gates, Thorndike confined them in "puzzle boxes" that could be opened in various ways to allow the animal to escape and find food. In his experiments on imitation, a cat or a young chick was allowed to learn by itself, by trial and error, how to escape. Then a second, observer animal watched. If observers learned faster than demonstrators, imitation must have occurred. Thorndike's experiments with cats and chicks provided no evidence for imitation, but he did leave open the possibility that monkeys would imitate, a possibility that continues to be debated.

13.3.2 Birds and the two-action test

Because one animal's behavior can come to resemble another's in so many ways, imitation sometimes seems to be what's left over when all other conceivable routes for social learning have been ruled out (Zentall 1996, 2006a). An experimental approach that goes a long way to ruling them out was pioneered by Thorndike (1911/1970). A puzzle box had two escape routes, and a chick watched another chick using one of them. If the observer chick imitated it should follow the same route as the demonstrator rather than the alternative, equally easy, one. In the more refined version developed by Dawson and Foss (1965; see also Galef, Manzig, and Field 1986), this design is known as the *two-action test* (Zentall 1996; Heyes 1996). Two-action tests typically involve an object, sometimes a tool, that can be operated on with either of two responses such lifting versus pushing or twisting versus pulling. Ideally both responses move the object in the same way. Otherwise, observers may copy the model not because they imitated its behavior but because they *emulated* or *learned the affordances* of the object (see Box 13.1).

Emulation tends to be invoked when observers copy demonstrators only crudely. For example, observer chimpanzees learned more quickly to use a tool to rake food into the cage than did controls that had not seen the tool being used, but they did not use the same technique as the demonstrator (Tomasello et al. 1987). *Emulation* has come to have a confusing variety of meanings referring to different kinds of learning thought to underlie the behavior (Box 13.1 and Whiten et al. 2004). Observers may have learned that there is a reward to be obtained or that the object is related to obtaining the reward. An associative analysis (Heyes 2005; Papineau and Heyes 2006) would see the first of these as situation-outcome learning and the second as object-outcome learning. Apparent emulators may have learned the object's affordances, that is, that it can be moved in a certain way, although how this learning could translate into behavior causing that same motion is itself mysterious (Zentall 2004). In any case, some birds as well as primates (Hopper et al. 2008) show affordance learning. For example, when pigeons saw a door move away from a food tray either to the left or to the right, they later more often pushed it in the direction they saw than in the opposite direction (Klein and Zentall 2003). Finally, an observer with theory of mind might infer the demonstrator's intentions and copy those, a process also sometimes referred to as *goal emulation* (see Whiten et al. 2004). However, given the paucity of more direct evidence for theory of mind in nonhuman animals (Chapter 12), there seems to be no good reason to invoke it here whatever the results of tests of imitation. As Heyes (1993a, 1008) put it, "What is apparently essential for imitation is that the imitating animal represent what the demonstrator did, not what it thought." The same can be said of emulation.

Some birds imitate in two-action tests (Zentall 2004). Many of these demonstrations involve a treadle that can be depressed by pecking it or stepping on it. Importantly, pecking and stepping are perceptually opaque responses that differ in topography but cause the lever to move in the same way. In one of the first studies with quail, for example, each subject was trained to eat from the feeder in the demonstrator's compartment before being placed in a neighboring compartment to view a demonstrator either peck or step on the treadle and receive food reinforcers for 10 minutes (Akins and Zentall 1996). When observers were returned to the response half of the chamber immediately after this experience, every bird's first response to the treadle matched the responses it had observed. In the first five minutes of the reinforced test, on average about 90% of the responses to the treadle were imitative responses (Figure 13.11). Of course (see Heyes 1996; Whiten et al. 2004) the birds' behavior does not strictly qualify as imitation because the motor patterns being copied are not novel and unusual behaviors for the species. Nonetheless, considerable progress has been made in analyzing the learning of quail and pigeons in this situation (see Zentall 2004). Importantly (see Box 13.1), imitative behavior does not depend on being tested immediately; in quail it is also evident in a test delayed 30 minutes, more consistent with learning than some sort of temporary facilitation (Dorrance and Zentall 2001).

The robust copying of pecking and stepping sets the stage to discover what the animals actually learn from watching. Because the treadle moves in the same way whether it is pecked or stepped on, the birds must have acquired some representation of the observer's action. Does it matter if the demonstrator is seen to be rewarded for its efforts? Studies with quail indicate that little imitation occurs if either demonstrators are not hungry or observers are not rewarded (Zentall 2004). However, this does

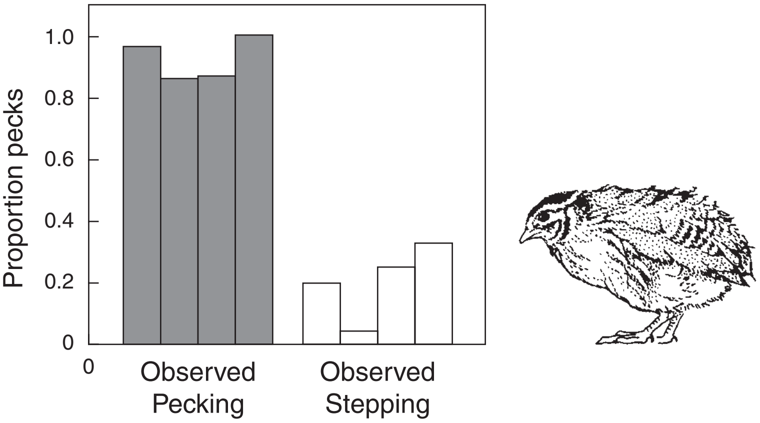


Figure 13.11. Proportion of individual quails' responses to a lever that were pecks during the first five minutes of a two-action test. Redrawn from Akins and Zentall (1996) with permission.

not necessarily mean that observers are learning response-food associations by observation; being hungry and seeing the demonstrator getting food might only increase the observer's attention to the demonstration. Indeed, there is evidence for blind imitation in this kind of situation (i.e., copying the observer regardless of the outcome it is getting), at least with already-trained responses. Pigeons that have been shaped both to peck and to step on a treadle and then watch a demonstrator pecking or stepping subsequently increase their own tendency to perform the same action, whether or not the demonstrator was being rewarded (McGregor et al. 2006). In a similar test in which the demonstrator pecks in the presence of one colored light and steps in the presence of another, pigeons acquire the observed stimulus-response associations (Saggerson, George, and Honey 2005). It is not yet clear whether these findings means that pigeons (and perhaps other birds) always engage in blind imitation or whether imitation is goal-directed under some conditions (McGregor et al. 2006).

As mentioned earlier (Section 13.1.2), social learning is more likely to be adaptive if animals do not always do what others are doing. But the fact that blind imitation occurs when all other factors that might be relevant are tightly controlled does not mean it would lead to maladaptive consequences in nature. For example, in the study of McGregor et al., observers were not rewarded in the test; they might not have copied the demonstrator for long if reward had been available for some alternative behavior. In any case, this series of studies is an important beginning to understanding the conditions for learning by imitation. Further insights come from recent studies of primates.

13.3.3 Chimpanzees and children

Until the last decade or so of the twentieth century, most evidence regarding imitation in monkeys and apes consisted of anecdotes from the field or from captive animals reared in close association with humans (Whiten et al. 2004). Because human children seem to be good imitators, our closest living relatives were assumed to be good imitators too. Indeed, in many languages the same word (e.g., *ape*) refers both to a nonhuman primate and to the act of imitating (Visalberghi and Fragaszy 1990a). The assumption that apes *can* ape led to skepticism about suggestions that they do not ape very readily or exactly and to a lack of experimental tests of imitation in primates. The situation has changed dramatically in the last 15 to 20 years. A recent review lists over 30 studies of apes (Whiten et al. 2004), and that does not include a more recent spate of direct comparisons between chimpanzees and children (e.g., Call, Carpenter, and Tomasello 2005; Horner and Whiten 2005; Herrmann et al. 2007). These studies are important not only for how they illuminate mechanisms of imitation but also for what they imply about human cognitive uniqueness and the abilities that support human culture.

A breakthrough here was an experiment by Whiten et al. (1996). These researchers both gave chimpanzees a two-action test of imitation and tested young children under the same conditions (see also Nagell, Olguin, and Tomasello 1993). Moreover, their task—opening an "artificial fruit"—resembled foraging behaviors chimpanzees might learn by imitation in the wild. The artificial fruit was a transparent plastic box containing a food treat which could be opened by manipulating various handles or bolts (Figure 13.12). In one version the lid was closed by two bolts that could be either poked or twisted out. Captive chimpanzees or 2-, 3-, or 4-year-old children saw a human adult poke or twist the bolts and then were given a similar "fruit" that could be opened using either action. Subjects' behavior was videotaped and scored independently by two observers ignorant of which action the subjects had witnessed. Subjects of both species were significantly more likely to use the action they had seen than the alternative (Figure 13.12). The tendency to imitate was least in the chimpanzees and greatest in the 4-year-old children. The children were more likely than the chimpanzees to copy slavishly even nonfunctional parts of the demonstrator's acts, as if taking for granted that an adult's way of doing things is worth copying. The chimpanzees did direct their behavior at the correct part of the box even when they

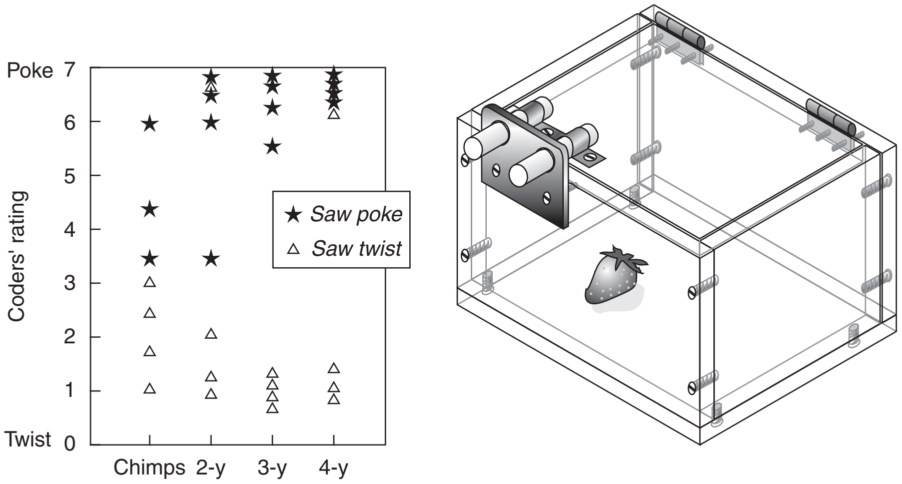


Figure 13.12. Coders' ratings of the performance of chimpanzees and 2-, 3-, and 4-year-old children presented with the artificial fruit at right as a function of whether the subjects had seen a human adult demonstrator poke or twist the bolts. Each data point represents one subject, rated on a 7-point scale as to whether actions on the bolts more resembled poking or twisting. Redrawn from Whiten et al. (1996) with permission.

did not use the same actions they had seen, that is, emulating or showing they had learned the affordances of the apparatus (the bolts come out; the box opens).

One of the first questions these findings raise is whether the chimpanzees would copy more precisely with a chimpanzee rather than a human demonstrator. The answer to this question seems to be “no” (Whiten et al. 2004). Given that the chimpanzees did show some copying of the demonstrated actions, another question is what determines the extent to which they imitate specific actions as opposed to emulate or learn affordances? One suggestion is that imitation plays a greater role in more complex tasks. Conversely, nonsocial processes such as affordance learning appear more important in simple tasks. This latter conclusion is supported by a comparison of two separate studies in which chimpanzees watched devices move by themselves (as if moved by a ghost, hence *ghost conditions*). Using a scaled-up version of Klein and Zentall’s (2003) apparatus for pigeons, Hopper and colleagues (2008) had chimpanzees and children watch the door on a box move to the left or the right to reveal food inside (Figure 13.13). The effects of this experience on subjects’ subsequent actions on the door were compared to the effects of watching either the door move by itself in the presence of a conspecific who then retrieved the food (“enhanced ghost condition”) or a conspecific pushing the door (full demonstration). Chimps and children in all conditions were very likely to push the door in the demonstrated direction on their first opportunity. However, all the children continued to prefer the demonstrated direction, whereas the chimpanzees maintained this preference only if they had seen a chimpanzee doing the pushing. Still, their initial responses are evidence that they learned the affordance of this simple apparatus in which the part to be moved was very close to the food. These results contrast with those obtained when a more complex task was used in a test of social transmission within chimpanzee groups (see Section 13.5 and Hopper et al. 2007). Here a stick had to be used to lift a T-shaped bar on top of a box so that food would roll out at the bottom of the box. Only one of 18 chimpanzees exposed to a ghost condition operated the apparatus successfully in a subsequent 1-hour test. A larger proportion of successes followed demonstrations in which a chimpanzee lifted the T bar. However, this was a

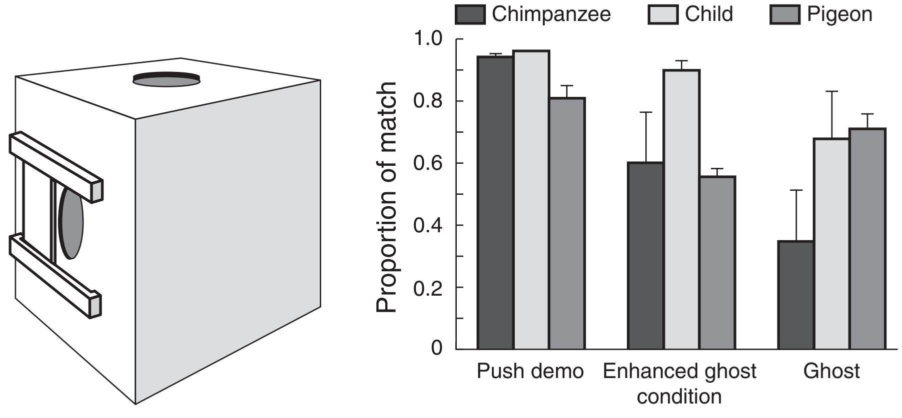


Figure 13.13. Apparatus used for two-action tests of chimpanzees, children and pigeons. Subjects saw the sliding door on the front of the box moved to the left (as shown) or the right. Data are mean proportion of their own attempts to push the door in the same direction. Hole in the top of the box is for inserting the food. After Hopper et al. (2008) with permission.

difficult task in that there were relatively few successes compared to those in an alternative version in which the food was released by poking the tool into a hole.

Although increased task difficulty (and perhaps remoteness of the reward from the object to be moved) seems to reduce affordance learning or emulation, it seems to enhance learning by imitation. Perhaps the most striking evidence for this conclusion comes from another comparison of chimpanzees and children (see also Call, Carpenter, and Tomasello 2005; Horner and Whiten 2005) involving copying several actions in sequence, a capability for which there was already some evidence from chimpanzees (Whiten 1998) and gorillas (Stoinski et al. 2001). Here both chimpanzees and 4-year-old children watched a human adult use a stick to perform one of two sequences of actions on the box shown in Figure 13.14. The only functional part of these sequences involved sliding or lifting the door in the front of the box and pulling out a packet of food with the stick. The demonstrator began, however, by tapping the bolt on top of the box, then moving it aside to reveal a hole and thrusting the stick into the hole. These actions were done in a slightly different way for each of two subgroups, making this as well as the sliding versus lifting of the door a two-action test. In either case they were irrelevant to operation of the box because a barrier separated the top half of the box from the food. Their causal irrelevance was evident in a transparent version of the box but not in an opaque one. Subjects of both species frequently copied the sequence of actions they saw, but the most important result of this study is that whereas the children imitated the irrelevant action of inserting the tool into the top of the box about 80% of the time whether the box was opaque or clear, the chimpanzees did so much more often when the box was opaque (Figure 13.14). If exposed and tested with the clear box, they most often bypassed this part of the sequence and went straight to operations on the door over the food. The authors interpret this finding to mean that when the causal structure of the task was evident the chimpanzees emulated, that is, primarily relied on learning about the results of actions.

It is not clear from this experiment alone, however, whether the animals' ability to see the effects of the irrelevant actions affected learning or performance. Perhaps they learn about both the actions of the demonstrator and the goal that can be obtained

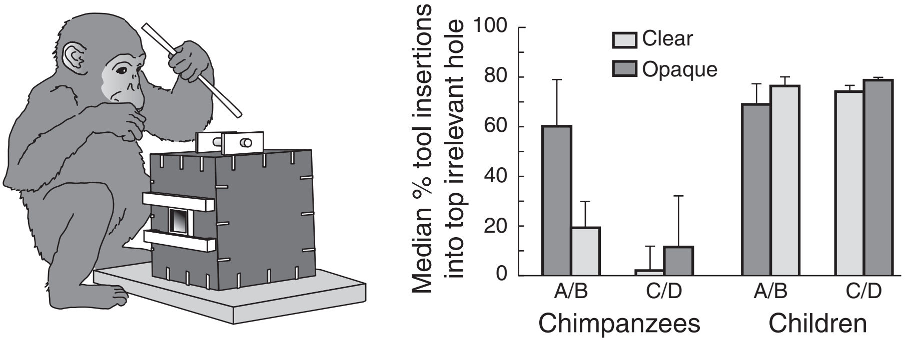


Figure 13.14. Apparatus for testing copying of a sequence of actions by children and chimpanzees, here in the opaque version. Copying the human demonstrator's action of inserting the stick tool into the top of either box, as this subject is about to do, is functionally irrelevant to obtaining reward, which is behind the door on the side. A/B and C/D refer to different orders of presenting an opaque and a clear box, as explained in the text. After Horner and Whiten (2005) with permission.

but goal-related cues take precedence in control of behavior when they are very salient. Animals trained first with the opaque box could learn from observation and personal experience about the food-containing part of the apparatus that lay behind the door; once they could actually see it through the transparent box, direct approach evidently took precedence over imitating earlier parts of the sequence (group A/B in Figure 3.14). Animals trained first with the transparent box continued to go directly to operating the door when given trials with the opaque box (group C/D), but of course by then they had a history of immediate reward for these actions. Interestingly, however, whatever else they did all animals had a significant tendency to move the door in the way they had seen it moved by the demonstrator.

Horner and Whiten (2005) discuss their findings in the spirit of an analysis of human imitation proposed by Wohlschla?ger, Gattis, and Bekkering (2003). This starts from realizing that a demonstration of a complex action on an object has several distinct elements including not only the actions but the object(s), and the outcome of the actions (i.e., the affordances of the object and/or rewards for the demonstrator). Attention to actions may result in imitation, but an observer might instead attend to and learn about the object and/or the outcome. In any case, when the observer confronts the task alone later, memory of one or more of these features will be activated and this in turn will elicit relevant motor programs (for example, copying the action, interacting with the object, trying to obtain the goal directly). Wohlschla?ger and colleagues (2003) propose that the goal of the action always takes highest priority in controlling the observer's behavior. However, priorities vary with the direction of attention, as shown by Bird et al. (2007). People were asked to copy the actions of a model who grasped a pen and placed it into one of two nearby cups. Different elements of this simple demonstration were made more or less distinctive and subjects' copying errors were measured. For example, when the model's hands had differently colored gloves and the cups did not differ in color, subjects made fewer errors in copying which hand to use and more in copying the cup than when the reverse was true.

Bird and colleagues (2007, 1166) conclude that, "the mechanisms that mediate imitation are plastic with respect to the processing of ends and means. Furthermore, the factors influencing which aspects of an action are imitated are task general." Similarly, Horner and Whiten (2005) suggest that chimpanzees attend to different aspects of a demonstration in different circumstances, and imitation, emulation, or something else predominates accordingly. Children, however, seem to have a consistent bias toward imitation (see also Want and Harris 2002). Whether this represents a predisposition present from a very young age and how much it is enhanced by the experience of being constantly shown things by adults is a matter of debate. Moreover, under some conditions young children do not slavishly copy unusual actions of a demonstrator but do the same thing with a different action, as if copying the demonstrator's intention (Gergely and Csibra 2003) or engaging in goal emulation. In any case, an account of variations in chimpanzees' tendency to imitate in terms of variations in attention or memory explains everything and nothing. Experiments with chimpanzees like those of Bird et al. (2007) in which factors known to influence attention are manipulated without otherwise changing the structure of the task being demonstrated will be required to test it.

13.3.4 Do monkeys ape?

Insofar as they have been tested, the other three great ape species (gorillas, orangutans, and bonobos) behave similarly to chimpanzees: they imitate to some extent but may copy in other ways too (Whiten et al. 2004). In contrast, there is very little evidence that monkeys of any species imitate in the narrow sense of copying specific actions they have witnessed (Fragaszy and Visalberghi 2004). An exception is the performance of marmosets in a two-action test (Voelkl and Huber 2000). After seeing a demonstrator marmoset use either its mouth or its hand to pull the lid off a film canister and get food inside, observers were more likely to use the action they saw than the alternative. More typical is the finding that capuchin monkeys exposed to conspecifics that were proficient at using a stick to get reward from a tube in the task described in Chapter 11 showed no evidence of imitating them (see Fragaszy and Visalberghi 2004). But notwithstanding their evident failure to copy exactly the actions they have witnessed, many monkey species do show various kinds of social influences on learning (see Fragaszy and Visalberghi 2004). This propensity may lead to social transmission of tool use and other behaviors in some wild monkeys (Section 13.5). In the laboratory, monkeys have provided the only evidence for two novel kinds of imitative learning. In one case, rhesus macaques looked longer at a person who was copying their actions on a novel object than at a second person who handled the object at the same time but did different things with it (Paukner et al. 2005). Thus even though they do not imitate the actions of others very well, monkeys apparently notice when another is imitating them.

In the second novel form of imitation, one of two experienced rhesus macaques watched from an adjoining operant chamber while the other one executed a simultaneous chain that was novel for the observer (Subiaul et al. 2004). In the simultaneous chaining task (Section 10.3), the animal learns to touch a series of arbitrary images in a fixed order. By what the authors call *cognitive imitation,* the observer could learn not the required actions, which in any case varied from trial to trial with the positions of the images on the touchscreen, but the correct sequence of images. Both monkeys in this study showed cognitive imitation in that they completed the first trial of a new sequence with fewer errors after watching the knowledgeable partner than under various control conditions, including exposure to a computer replay of the sequence of images and sounds generated by a knowledgeable partner. Two-year-old children also show cognitive imitation in this task (Subiaul et al. 2007). Learning sequences of actions in this way may have contributed to the performance of subjects in some of the multistage tool-using tasks described earlier.

13.3.5 Other candidates for visual imitation

Although imitation must ultimately be studied with experiments on groups of subjects, it is pretty compelling to see even a single animal do something like put on lipstick or use a tool in a way it has seen humans do. In a sense these are "multiple action tests" because there is a multitude of things the animal might do at the time. The literature on imitation by primates is full of accounts of such behaviors, mostly by chimpanzees and orangutans that have lived closely with people (see Whiten and Ham 1992; Whiten et al. 1996). One of the first of these was the chimpanzee Viki, raised like a child by the psychologists Keith and Cathy Hayes (Hayes and Hayes 1952). The Hayeses demonstrated that Viki had a fairly general ability to imitate novel actions by training her to obey the spoken command, "Do this." Custance, Whiten, and Bard (1995) trained two laboratory-reared chimpanzees in a similar way to the Hayeses but documented the procedures and results more fully. The animals were reinforced for obeying "Do this" using a set of fifteen actions like raising the arms, stamping, and wiping one hand on the floor. After more than three months of intensive training, they reproduced these actions with 80% accuracy or better. In a test with 48 other actions, observers who did not know what the model was doing could classify the chimps' actions at better than chance levels, but the agreement was far from perfect, suggesting that the animals were still not very good generalized imitators.

A host of accounts of orangutans reproducing complex human activities like using hammers and paintbrushes, constructing bridges out of logs, and making fires (!) comes from observations on formerly captive orangutans being rehabilitated for release in the Indonesian jungle (Russon and Galdikas 1993, 1995). Observations of complex imitations are not confined to primates, either. Alex the parrot learned to talk by watching two people, one of whom played the role of parrot and was rewarded by the other for pronouncing and using words correctly (Pepperberg 1999). This situation is thought to reproduce the social situation in which wild parrots acquire vocalizations. However, once Alex began to vocalize himself, he received attention, food, and/or access to the objects he was naming, and in any case vocal imitation is usually treated as a special case (see Box 13.2).

Explicit reward was scrupulously avoided with another parrot, Okichoro, trained by Moore (1992) to vocalize and imitate associated movements. The bird lived alone in a large laboratory room and was visited several times a day by a keeper who performed various stereotyped behavior sequences such as waving while saying "ciao" or opening his mouth and saying "look at my tongue." Gradually Okichoro, observed continuously on closed-circuit TV, began to imitate both the actions and the words of the keeper while he was alone (Figure 13.15). Because each vocalization in effect labeled a specific movement, possible imitation could be isolated from the stream of nonimitative behavior. And unlike pecking or stepping in quail, behaviors such as waving a foot while saying "ciao" are normally highly unlikely. Eventually many cases of imitation were recorded, including some nonvocal mimicry of sounds. For instance, the parrot imitated someone rapping on the door by rapping its beak on a perch. Moore (1996) claims that this is a special category of imitative learning, one of several that have evolved independently.

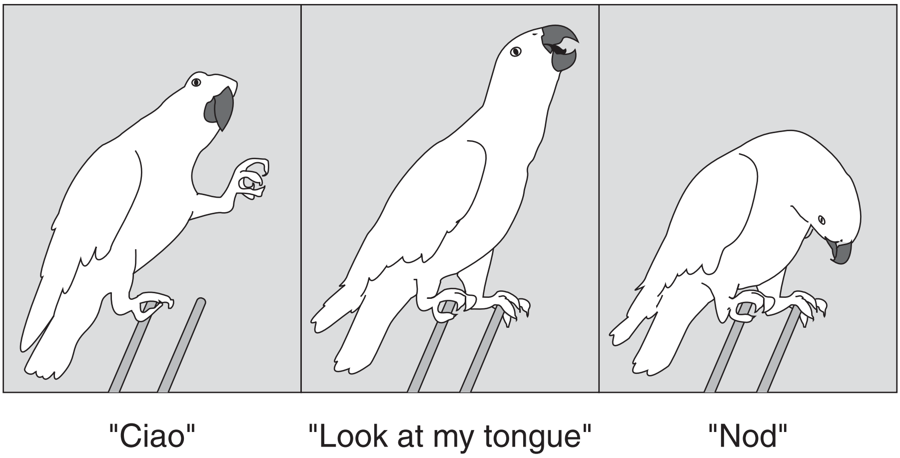


Figure 13.15. Okichoro performing some of his imitations. Each action was accompanied by a vocalization as indicated. After photographs in Moore (1992) with permission.

Although they are entertaining, such examples are prone to the weaknesses that afflict most anecdotal evidence. First, they are often based on a very special single subject. We may not know the animal's history. Was it reinforced for approximations to the purportedly imitated behavior or similar actions in the past? This lack of necessary background information very often characterizes isolated observations in the field, but studying animals in captivity is not always the solution. As with Alex or the orangutans, lengthy and complex experience often precedes the behaviors of interest. Even if every effort was made to control this experience, we rarely know precisely what it was. It may also be difficult to determine how selective the observers were in recording the subject's behavior. For instance, in a "do this" test, as opposed to a two-action test, the alternatives to reproducing the model's behavior may not be clearly specified nor is the time interval within which the animal must imitate as opposed to doing something else (Zentall 1996). Like the proverbial band of monkeys who would reproduce the works of Shakespeare if left long enough in a room full of typewriters, primates raised in homelike environments have many opportunities to perform humanlike actions, and those that are most humanlike and striking are most likely to be the ones reported. For example, how often did the formerly captive orangutans do something *inappropriate* like bite a paintbrush, hold it by the bristles, or hit a nail with it? Finally, the observers—for the very reason they are living closely with the animals in the first place—may be biased like proud parents to anthropomorphize what they see their animals do. Another problem for long-term research with one or a few subjects is the possibility of "Clever Hans" effects (Chapter 10), that is, the possibility that the observer is unintentionally influencing the subjects to produce the desired behavior. Unfortunately, being aware that such effects can occur is not necessarily enough to prevent them, and if the relevant contingencies are not detected by the investigators themselves, they may be difficult or impossible for others to detect in published reports.

The reports of imitation summarized here do not necessarily suffer from all, or even any, of these problems. Moore rigorously avoided Clever Hans effects by collecting data only over closed-circuit TV when the parrot was alone and by stopping data collection on any imitation once it had occurred in the presence of the experimenter. The rehabilitant orangutans imitated some elaborate sequences of behavior that were actively discouraged, like stealing boats and riding down the river (Russon and Galdikas 1993). Nevertheless, when assessing either anecdotes from the field or long-term work with a few subjects in captivity it is important to keep such potential problems in mind.

13.3.6 How is imitation possible?

Mirror neurons

How is it possible for me to perform the same action I see someone else perform, especially when that action is perceptually opaque? For example, when quail see other quail step on a treadle, how is it that they themselves later step rather than peck? This is *the correspondence* (Brass and Heyes 2005) or *translation* (Rizzolatti and Fogassi 2007) *problem.* A solution at the neural level is suggested by one of the most remarkable discoveries of late twentieth-century neuroscience, the *mirror neuron system.* This is a network of cells in the premotor cortex, inferior parietal lobule (IPL) and elsewhere in the brains of rhesus macaques that fire *both* when the monkey performs an action itself *and* when it sees the action performed by another. These actions include not only perceptually transparent actions such as grasping and

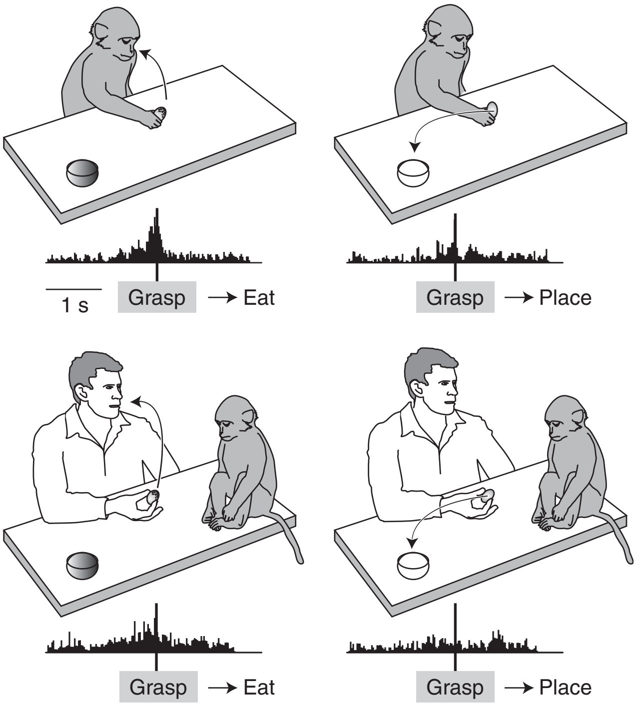


Figure 13.16. Mirror neurons distinguish between grasping a food pellet to eat it and grasping a nonfood item to place it in a bowl, as shown by the histograms of firing rate versus time below each drawing (data from Fogassi et al. 2005). Note how the neurons shown fire in the same way whether the actions are done by the monkey itself or by a person and that they fire *before* the action is performed (dark vertical bars), suggesting they could code intention. After Nakahara and Miyashita (2005) with permission.

tearing, but actions of the mouth such as biting and sucking (review in Rizzolatti and Fogassi 2007). Some mirror cells respond to auditory as well as visual correlates of actions, for instance firing both to the sound and the sight of paper being torn. In effect cells in the IPL encode not only the surface features of actions but their intent. The same cells that fire most when the monkey or a person reaches toward an object to grasp it also fire when a person reaches toward an object that the monkey has seen placed behind an occluder, making the grasping action invisible, but they do not fire in the absence of an object to be grasped. And in the example in Figure 13.16, grasping an object to eat it is distinguished from grasping to place it in a bowl, whether the monkey itself or a person does the grasping (Fogassi et al. 2005).

The mirror system evidently includes sensory-motor links between the visual and other cues accompanying performance of an action and its motor representation. Brain imaging shows that humans have a mirror system too (Rizzolatti and Fogassi 2007), and experience influences the strength of its sensory-motor links. For example, watching classical ballet is accompanied by greater activation of the mirror system in ballet dancers than in capoeira dancers, and the reverse (Rizzolatti and Fogassi 2007). Even experience over a relatively short term can have an effect (Catmur, Walsh, and Heyes 2007).

Here then is a remarkably rich neural representation of actions as such, encoding own and others' actions in a unitary way. Mirror neurons seem to be just what is needed to generate imitative behavior, but something must be wrong with this idea because, as we have seen, monkeys are not very good imitators. Instead mirror neurons may play some more general role in social cognition by encoding the actions and intentions of others as, in effect, the same as one's own (Rizzolatti and Fogassi 2007; de Waal 2008; but see Jacob and Jeannerod 2005). Still, the mirror system does seem to play a role in imitation in humans, for example being more activated during imitative than control tasks (Brass and Heyes 2005; Rizzolatti and Fogassi 2007).

One difference between monkey and human mirror systems that may underlie species differences in imitation is that the human system seems to encode specific actions more precisely (Rizzolatti and Fogassi 2007). A second difference may be in the degree to which motor output of the mirror system can be engaged selectively. If viewing another's action generates the same premotor activation as one's own intent to perform that action, then some further mechanism must prevent continual automatic and perhaps even dangerous mimicry. On one view (see Rizzolatti and Fogassi 2007) the primary function of the mirror system in all primates is to permit action understanding, not imitation. The flexible inhibitory mechanisms of the human prefrontal cortex permit its selective use to generate imitative actions, whereas in species that lack such mechanisms imitation needs to be inhibited in general.

Associative sequence learning

Consistent with evidence for an influence of experience on representation in the mirror system is a model of imitation developed by Cecilia Heyes (Heyes and Ray 2000, Heyes, 2005). In the associative sequence learning (ASL) model, imitation is the outcome of general associative mechanisms rather than a specialized ability, and it depends on experience during development (Brass and Heyes 2005). The elements of the model are so-called *vertical associations,* associations between sensory and motor activity correlated with one's own perceptible actions, for example the sight of one's own hand grasping and the motor commands to grasp. When an individual observes a sequence of actions performed by a demonstrator, the sequence is encoded as a set of *horizontal associations,* that is, associations within the sensory side. Now an action that is represented as such a chain of sensory-sensory associations will excite the associated motor representations, and, hey presto, the observer reproduces the sequence of actions it saw.

The ASL model can also explain copying of perceptually opaque actions such as pecking or stepping in quail and pigeons. The ASL model assumes that these flock-living birds will have been in situations where all the individuals present are engaged in the same behavior, for example pecking at grain. Such experience allows a bird to associate its own pecking with the sight of others pecking. When it later sees a demonstrator pecking in a certain experimental context it forms a context-other's pecking association. The vertical association between other's and own pecking in turn activates its pecking behavior. This explains why quail and pigeons are good at copying species-specific behaviors. It also may explain the population differences in sensitivity to different kinds of demonstrators documented by Lefebvre and colleagues (Section 13.2.3; Heyes and Ray 2000). It also suggests that experimental manipulations of social experience should influence what and from whom such birds copy, a suggestion that does not seem to have been tested. However, although it does a good job with copying of familiar actions, the ASL model does not seem to account for the essence of true imitation, namely the copying of novel actions as was done by Okichoro. Decomposing such actions into simpler actions which have been performed with conspecifics would seem to make this "simple" account of imitation quite a bit more complex, perhaps unacceptably so.

13.4 Do nonhuman animals teach?

Animals clearly learn from one another's activities or the products of those activities, even if not by imitation. So do any nonhuman species engage in behavior that could be called *teaching?* In humans, teaching seems to involve theory of mind and intentions to modify the pupil's behavior, but just as with *deception, planning,* and similar terms, when it comes to other species we need a clear operational definition that captures the essentials of the relevant behavior without mentalistic implications. In recent years, the accepted functional definition of teaching has been that proposed by Caro and Hauser (1992). To qualify as teaching, an animal has to meet three requirements. *(1)* It must modify its behavior specifically in the presence of naive individuals in such a way as to facilitate their learning. *(2)* The teacher should incur some immediate cost to itself, or at least no immediate benefit. But of course for teaching to evolve the teacher needs to reap some benefit in the longer term, such as reduced time feeding young or increased inclusive fitness due to having knowledgeable offspring. *(3)* As a result of the teacher's behavior the pupil should learn something earlier in life or more rapidly than it would otherwise or that it would not learn at all.

Discussion of teaching thus shifts the focus from processes in naive individuals in a social group to those in experienced ones. Do the latter respond to correlates of ignorance in others by behaving so as to correct it? How are those responses, if any, tailored to the social learning mechanisms in potential pupils? And even if not theory of mind or intentionality, are any distinctive cognitive processes involved in it?

None of the examples of social transmission of information yet reviewed in this chapter meets Caro and Hauser's first requirement. A bird mobbing an owl is not teaching naive individuals what to mob because as far as is known it would be mobbing whether or not they were present. Similarly, rats transmit flavor preferences by serving as passive vehicles for stimuli that other colony members encounter during routine mouth-to-mouth contact. But perhaps teaching is more likely to evolve when the behaviors to be acquired are more demanding and complex than these. Caro and Hauser (1992) described a number of candidates involving capturing prey that are difficult to subdue or handle. For example, domestic cats bring dead birds and mice back to the nest and present them to their kittens. As the kittens mature, mother cats carry back live prey and allow the kittens to play with it, but if the prey escapes the mother still catches it again. Finally the kittens capture prey by themselves with little intervention from the mother. Cheetahs behave similarly. Osprey, which snatch fish from the water in their talons, have been seen apparently teaching their fledglings to forage. However, in none of these cases was it demonstrated what or how much the young actually learn as a result of the adults' behavior. This gap has been filled by a study of meerkats (*Suricata suricatta;* Thornton and McAuliffe 2006), a unique model demonstration of animal teaching.

13.4.1 Meerkats

Meerkats (or suricates, *Suricata suricatta;* Figure 13.17) are small cooperatively breeding mammals found in the dry parts of Southern Africa. They hold group territories in which the young are mostly produced by a dominant male and female but reared by all members of the group. When meerkat pups are about a month old, they begin to follow foraging groups around, making begging calls which stimulate older animals to bring them prey. These prey include scorpions, which are difficult or even dangerous to handle. Helpers often kill or disable such prey before presenting them to the youngest pups. Scorpions are killed or disabled for the pups to a greater extent than are other prey, but over the next two months all kinds of items are increasingly presented intact, as if the helpers are sensitive to the pups' growing

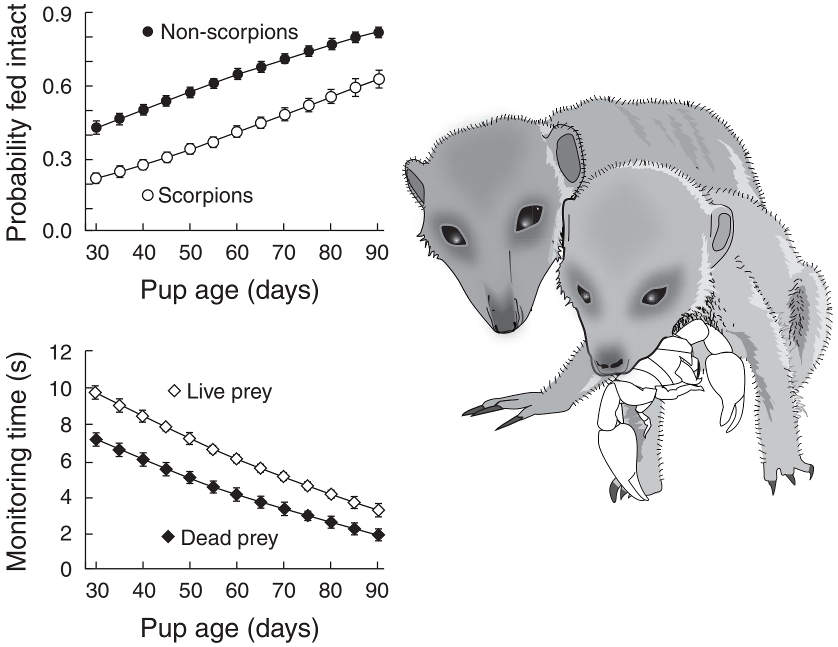


Figure 13.17. An adult meerkat watching a pup eating a scorpion and two effects of pup age on adults' behavior: as pups grow older adults feed more intact prey and spend less time monitoring the pup with the prey. Adult behavior is also appropriate to type of prey throughout. After a photograph provided by Alex Thornton and data in Thornton and McAuliffe (2006) with permission.

competence(Figure 13.17). The pups' age is reflected in their begging calls, and a playback experiment showed that this proxy for pup competence determines the proportions of prey offered in different states. In groups with young pups, calls of older pups elicited more provisioning of intact prey, whereas in groups with older pups, begging calls of young pups increased the number of dead prey provided. In addition to spending foraging effort on obtaining prey for pups, helpers stay nearby for a few seconds after delivering a food item. They stay longer with younger pups, and if a pup of any age does not take an item immediately, they may nudge it, as if drawing the pup's attention. If the prey escapes, the helper recovers it and presents it again.

Thornton and McAuliffe's (2006) extensive observational data together with the playback experiment demonstrate that the helpers' behavior fulfills Caro and Hauser's first two criteria for teaching: it is conditional on the presence (and here, age) of ignorant others and costly in time and effort in the short term. The results of a further experiment show that it also meets the requirement of aiding pup learning. Thornton and McAuliffe (2006) compared three groups of pups matched for age and litter in their treatment of a live but stingless scorpion after three days of supplementary experience with either four live scorpions presented daily by the researchers (a much higher number than normal), four dead scorpions, or equivalent amounts of hardboiled egg. Pups in the first group were markedly more successful in handling the test scorpion, consistent with the experience provided by provisioning "teachers" aiding their learning to subdue and process scorpions. The behavior of the experienced meerkats is therefore comparable to that of mother black rats in that it allows the young to acquire skill in processing a challenging prey item, but the meerkats respond to stimuli indicative of the pups' age (the begging calls) and experience (e.g., whether the scorpion escapes, is attended to, etc.) whereas the role of the mother rats in their pups' learning is mainly to tolerate them nearby and to drop partially eaten pinecones. In neither case however, do we need to invoke adults' understanding of the pups' mental state.

13.4.2 Pied babblers

Another recently described example illustrates how "teaching" may result from a specialization in particular parts of a more species-general kind of behavioral sequence. Pied babblers (*Turdoides bicolor*) are communally breeding birds found at the same study site in South Africa as the meerkats. As in many altricial species, adults feed the young birds in the nest for 2 to 3 weeks, and the family group forages together once the nestlings fledge. Also as in other altricial birds (e.g., Tinbergen and Kuenen 1939/1957), stimuli associated with an adult's arrival at the nest elicit begging by the otherwise quiescent nestlings. Raihani and Ridley (2008) observed that when pied babbler nestlings are 10 to 11 days old, arriving adults begin to emit a "purr" call. When they are about 13 days old, nestlings begin begging in response to purr calls. To show that nestlings' response reflects learning to associate purr calls with food rather than maturation, beginning when the nestlings were 9 days old Rahini and Ridley played purr calls at six nests whenever an adult arrived with food. All them begged in respond to recorded purr calls by the age of 11 days, whereas nestlings in unmanipulated broods did not respond to the same test until Day 13, and begging was seen in only one control that had heard purr calls in the absence of food delivery.

So far, pied babbler purr calling fits the first and third criteria for teaching: it occurs specifically in the presence of "pupils," and they learn something as a result, presumably a Pavlovian association between purr calls and food. It also meets the criterion of being costly to the "teacher." Purr calling is accompanied by fluttering of the wings, and the more that adults display purring and fluttering within a given time, the less weight they gain. But why should the nestlings learn to respond to purring? The adults feed them anyway, or at least they do so without purring for the first 11 days. The likely function of learning that purring signals food becomes apparent after the young leave the nest around the age of 20 days and accompany loose groups of foraging adults around the territory. Adults in such groups purr call more often than in groups that do not have fledglings (Radford and Ridley 2006). They purr when they have found food, in effect calling the young (as well as other adults) to approach, a response that in fact increases the nestlings' foraging success. Sighting a predator also elicits purr calling when fledglings are present, in effect calling them away from danger.

Unlike with the meerkats, where the availability of dangerous and hard to handle but large prey items might create an exceptional pressure for evolution of costly teaching, the situation experienced by the babblers seems much the same as that for other birds in which newly fledged young accompany adults while foraging. What seems special in the babblers, or at least not yet proven for other species, is the context-specific purr call. But food calling in domestic fowl and the ancestral Burmese red junglefowl has many similar properties (see also Section 14.2). In food calling, both hens and roosters pick up a morsel of food in the beak, lower the breast and spread the tail while uttering a distinctive call. Hens food call in the presence of young chicks (Sherry 1977). Food calls attract the chicks, and because chicks tend to peck where they see another bird pecking, the hen's food calling functions to cause the chicks to peck at the food, in effect teaching them what to peck at (see also Nicol and Pope 1996). Moreover, although they have a preexisting tendency to move faster toward a call given to high than to low quality food, chicks can learn the reverse discrimination (Moffatt and Hogan 1992). Thus although by Caro and Hauser's criteria the adult babblers are teaching the young that purring means food, much more could be done to understand whether or why this situation differs from that for many other species in which mobile young accompany foraging adults and use cues to food that they provide.

13.4.3 Teaching in ants?

Ants of the species *Albipennis bithorax* sometime engage in *tandem running* when going from the nest to food: one ant travels behind the other, the follower frequently touching the leader on her legs and abdomen. When leaders were established in a laboratory colony by letting them find food, and naive individuals were then allowed to follow them, leaders were observed to pause when a follower lost contact, as if waiting for the follower to catch up (Franks and Richardson 2006). Moreover, when a follower was removed partway through the trip, leaders waited longer before proceeding the more valuable the food source and the longer the trip had already been in progress (Richardson et al. 2007).

These observations have been interpreted as showing not only that ants teach but as suggesting an additional criterion for teaching, namely that the teacher should be sensitive to feedback from the pupil (Franks and Richardson 2006; Richardson et al. 2007). Be that as it may, leaders clearly meet some of the criteria for teaching in that they behave differently with than without a follower and pay a time cost by doing so. However, it has not yet been directly shown that anything is learned by followers in a tandem run, although some indirect evidence is available (Franks and Richardson 2006; Richardson et al. 2007). It remains to be demonstrated that once a follower has returned to the nest after a tandem run it finds the food again more quickly than a naive individual searching at random. This second trip of ants that have been "taught" the food's location should also be compared to that of ants that originally found it on their own to see whether the benefit, if any, from following is confined to the first trip to the food.

13.4.4 But what about primates?

The folk-psychological assumption that teaching requires cognitive complexity implies chimpanzees and other great apes should teach, but although some apes and monkeys have population-specific behaviors that may be socially transmitted (Section 13.5), there is essentially no evidence than any such behaviors are taught by experienced to inexperienced individuals. For example, in one population in West Africa chimpanzees crack coula nuts with stone hammers and anvils (Figure 13.18). In over 10 years of field work, Boesch (1991) observed hundreds of cases in which chimpanzee mothers "stimulated" or "facilitated" their infants' nut cracking but only two cases that might have been teaching. Stimulation consisted of leaving stone hammers near anvils rather than carrying them off. Facilitation meant providing both hammers and nuts to infants at anvils. Both of these behaviors changed with the ages of the infants. In the two cases of apparent teaching, the mother intervened with an infant attempting to crack a nut and positioned the tool or the nut correctly.

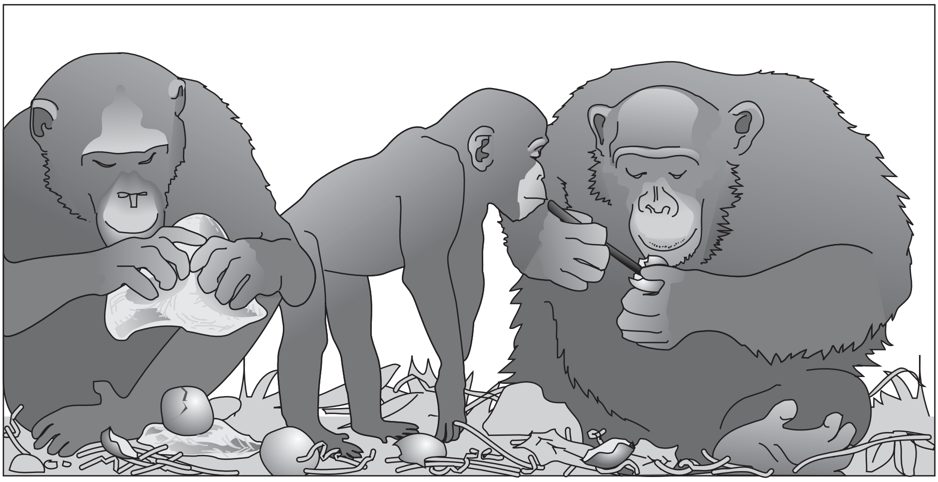


Figure 13.18. Adult chimpanzees cracking and eating coula nuts as a young one watches. After a photograph in Boesch-Achermann and Boesch (1993) with permission.

No indications of teaching or of imitative learning were found in a detailed analysis of the development of nut cracking in another area of West Africa (Inoue-Nakamura and Matsuzawa 1997).

At most, by exposing their infants to nuts and stones, nut-cracking mothers promoted interactions with stones and nuts by providing the conditions for stimulus enhancement. There is also little or no evidence that chimpanzees teach their offspring how to "fish" for termites with sticks. Indeed, although infants spend a lot of time watching their mothers extract termites and even get some of the insects to eat, as with nut cracking they seem to need a good deal of individual practice to become efficient fishers themselves (Lonsdorf 2005). And among the nutcracking capuchins described in Chapter 11, the young themselves make a major contribution to supplying interactions that might serve in social transmission of nut-cracking skills. They prefer to watch the most proficient adult nutcrackers, perhaps because that gives them the most opportunities to scrounge bits of nut (Ottoni and de Resende 2005).

13.4.5 Conclusions

As with deception or planning, demonstrations that candidates for animal teaching meet a clear functional definition are controversial because they seem to lack key components of analogous human competences (Leadbeater 2006; Csibra 2007). Babblers, meerkats, or ants apparently teach others at most one thing. This may not be inconsistent with the functional definition of teaching, but even if further research reveals a species that teaches in several contexts, in human teaching understanding the learner's state of knowledge or ignorance (i.e., using theory of mind) confers an ability to teach everything from tying shoes to doing physics (Premack 2007). In any case, the scattered phylogeny of species with behaviors that function to teach makes it unlikely that such behaviors are homologous with human teaching, that is, evolutionary precursors to it (Galef 2009). This distribution instead raises important questions about what kinds of life history and ecology favor selection for costly behaviors that provide learning opportunities for the young or inexperienced.

The analysis in this section suggests these will be on a continuum with other responses to such individuals, for example specializations in responses to the stimuli that elicit provisioning. There is no evidence so far of any cognitive abilities specific to teaching. And from the learner's point of view, behaviors of "teachers" provide opportunities for learning by trial and error (as in meerkats), observational conditioning (as in pied babblers), acquiring spatial information (as suggested for ants) or by some other general mechanism. In summary there is still no reason to question the conclusion stated many years ago by the ethologist R. F. Ewer (1969, 698), "it is preferable to think in terms of instinctive behavior patterns which produce learning rather than of the 'instinct to teach,' which, in any case, has subjective overtones. . . . The responses of the mother are simply those which provide the correct situation for evoking the developing repertoire of responses of the young who are thus enabled to educate themselves."

13.5 Animal cultures?

Whatever else it may mean, when applied to humans, *culture* refers to multifaceted groupwide traditions: population-specific behaviors, beliefs, and attitudes, transmitted from one generation to the next through language, teaching, and in many less explicit ways. The socially transmitted behaviors of nonhuman animals described so far such as food preferences in rats or enemy recognition in birds influence so few aspects of their lives as to be scarcely the rudiments of culture. But, in contrast to rats, birds, and most other animals, geographically separated groups of chimpanzees and orangutans show multiple, populationwide differences in acquired behavior that have been suggested to represent evolutionary precursors to human culture. The most substantial relevant data come from a collaboration among researchers doing long-term studies of chimpanzees at seven sites in Africa (Whiten et al. 1999, 2001). For each population, the local team estimated the frequency of occurrence of 65 behaviors, many of which involved tool use or other interactions with objects such as manipulating sticks in different ways to obtain ants or termites, using leaves to sponge up water. When a behavior had not been seen, a judgment was made as to whether there was an ecological explanation for its absence. For instance, termite fishing is impossible without termites. The most interesting cases are those 39 in which a behavior was judged relatively common in some populations but absent in others even though the ecological conditions for its appearance were judged to be present. Given that genetic differences among the populations can be assumed to be unimportant, such patterns suggest the behavior must have been discovered by one or more innovators and then acquired by others in the group by some kind of social transmission (i.e., any one or more of the mechanisms in Box 13.1).

Beginning with the titles of the original reports, these population differences in chimpanzees (Whiten et al. 1999, 2001) and orangutans (van Schaik et al. 2003) have been referred to as "cultural," but this description is much debated (Galef 2004; Laland and Janik 2006; Perry 2006; Whiten and Van Schaik 2007; Galef 2009). There are two basic sources of controversy. One, discussion of which is beyond the scope of this book, is that *culture* has a rich web of connotations in anthropology, archaeology, and a whole range of other disciplines, not to mention in folk psychology, and to some writers these are simply incompatible with the possibility of "animal cultures" no matter how apparently inoffensively and objectively defined. The other is that even if population-specific behaviors in nonhuman species are referred to instead as *behavioral traditions,* conclusive evidence is needed that the behaviors involved really are transmitted socially as the term *tradition* implies rather than learned individually or determined by ecological conditions, and field observations alone rarely if ever can provide such evidence (Galef 2004, 2009).

An analysis of "ant dipping" by chimpanzees shows how ecological factors favoring one behavior rather than another may not be obvious. In dipping for ants, a chimpanzee uses a stick or grass stalk to capture biting ants. The tool is moved back and forth to stimulate the ants to climb up on it. They are then removed either by putting the tool directly into the mouth ("direct mouthing") or by pulling it through the hand and putting the resulting clump of ants into the mouth ("pull through technique"). Ant dipping is a candidate cultural behavior because different techniques as well as different lengths of tools are prevalent in different populations. However, in one population, at Bossou, Guinea, chimpanzees use both techniques as well as both short and long tools. By combining observations of the conditions under which different tool lengths and removal techniques were used with experiments in which the researchers themselves dipped for ants, Humle and Matsuzawa (2002) showed that there are good functional reasons for these variations in dipping. It turns out that there are more and less aggressive species of ants; the ants are also more belligerent at the nest than when migrating along the ground. Using longer tools and the pull through technique limits biting by the ants, and it is the preferred technique for situations where ants are most aggressive. However, an analysis of behavior of ants at two sites with different patterns of ant dipping indicates that some of the population differences in ant dipping are likely to be cultural (Mobius et al. 2008).

A further issue is that no matter how compelling the observations of young animals watching adults using tools or the like (e.g., Figure 13.18), the occurrence of any kind of social learning or social influence on learning in such interactions needs to be tested experimentally. Given the paucity of convincing evidence for social transmission of wild chimpanzees' population-specific behaviors, researchers have turned to demonstrations that tool-using skills can be socially transmitted in captive groups (Whiten, Horner, and De Waal 2005; Horner et al. 2006; Hopper et al. 2007). These studies typically involve apparatuses like that used in two-action tests of imitation, introducing each technique for operating it into a different group of subjects. A third group may be left on their own to see whether one technique or the other, if any, is acquired spontaneously. With an "artificial fruit" having a door that could be lifted or pushed, a transmission chain was formed. Observer 1 learned the technique used by trained demonstrator, then Observer 2 learned it from observing Observer 1, and so on up to a chain of five or six chimpanzees. Some controls who saw food put into the box eventually opened it one way, some the other (Horner et al. 2006). Consistent with these findings, when a single trained demonstrator was introduced into whole group, most individuals learned the tool use task being demonstrated and used the same technique as the demonstrator (Whiten, Horner, and De Waal 2005). However, the robustness of a technique across a transmission chain may depend on the type of task (Hopper et al. 2007).

Monkeys, too, have what appear to be traditional behaviors (Perry and Manson 2003). Indeed, one of the oldest candidates for animal culture is potato washing by Japanese macaques (Box 13.3). More recently, wild white-faced capuchin monkeys have been observed in what are some of the best candidates for socially learned population-specific behaviors. These are rather bizarre and apparently arbitrary "games," such as monkeys taking turns putting their fingers into each others' mouth and getting a firm bite (Perry et al. 2003). It has been possible to trace the spread of some of these behaviors within and between groups. Social transmission of a foraging

Box 13.3 Sweet Potato Washing by Japanese Macaques

One of the most famous candidates for culturally transmitted behavior in free-ranging animals is sweet potato washing by Japanese macaques. A colony on Koshima Island was provisioned with sweet potatoes, and in 1953 a young female, Imo, was first seen taking sand-covered pieces of potato to a stream and washing the sand off before eating them (Kawai 1965; Nishida 1987; Hirata, Watanabe, and Kawai 2001). Over the ensuing years potato washing spread through the colony, first to animals closely affiliated with Imo (Figure B13.3). Although these observations were described in the secondary literature as an innovation invented by a young animal being imitated by social companions (e.g., Bonner 1980; Gould and Gould 1994), more critical thinking about social learning and animal traditions has challenged such conclusions.

One issue is whether the data in Figure B13.3 are actually consistent with social transmission. Any socially transmitted behavior might be expected to arise more or less by chance, spread slowly at first and then more and more rapidly as more models are available for naive individuals to learn from. It has typically been assumed that when, in contrast, individuals learn entirely on their own the number of individuals showing the behavior rises at a constant rate until all members of the group have learned. Clearly, the data shown here are more consistent with the second of these scenarios than with the first. Notice, too, that the time scale is years, suggesting that any social learning was very slow. However, the conclusion suggested by this analysis, due to Galef (1996a), was questioned by adding just one more data point, and by showing that the majority of twenty other cases in the literature on primates also show an accelerating function (Lefebvre 1995b).

The idea that the shape of diffusion functions, of which Figure B13.3 contains a simple example, may be used to discriminate social from individual learning in data from free ranging groups is appealing, but there are many problems with it (Reader 2004). Collecting all the relevant data for a given population may be no easier than collecting any other data on learning in wild animals. In addition, different assumptions about the processes of social and/or individual learning involved generate different diffusion curves. For instance, individual learning can lead to an accelerating function in a population with a normal distribution of learning ability. The number of skilled animals increases slowly when the group is first exposed to the task (for example, the provision of sweet potatoes) because the minority at the "high ability" end of the distribution learn first. It accelerates once enough time has passed for the majority of average ability to acquire the skill and slows down again when only the slowest learners are left (Reader 2004).

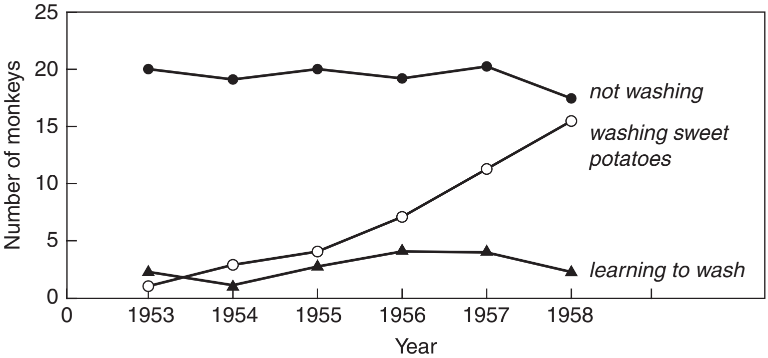


Figure B13.3. The incidence and spread of potato washing among Japanese macaques on Koshima Island between 1953 and 1958. Redrawn from Galef (1996a) with permission.

In any case, because sweet potato washing began over half a century ago, we will never be certain exactly what went on. There are suggestions that once washing had appeared in the colony, the keepers providing the sweet potatoes encouraged the animals to wash them (see Galef 1996a). The activities of knowledgeable individuals with food near water provided conditions under which their companions could discover food washing for themselves, for instance by picking scraps out of the water (M. Kawai 1965). Moreover, washing sandy food is not as unlikely a behavior among monkeys as it might seem. The macaques in the Kashima colony also separated grains of wheat from sand by dropping handfuls of sandy wheat in water, where the grains floated to the top and could quickly be gathered up, and several other examples of apparent cultural transmission involve washing food (Lefebvre 1995b). When Visalberghi and Fragaszy (1990b; see also Visalberghi 1994) provided individual captive tufted capuchins and crabeating macaques with sandy fruit and a tub of water, a number of them showed unambiguous food washing within a few hours. In conclusion, as in the examples in the main text, although potato washing may be a traditional or "precultural" behavior (Kawai 1965), its spread likely involved a variety of different processes.

technique along a chain of animals has also been demonstrated among captive capuchins with similar methods to those used for chimpanzees (Dindo, Thierry, and Whiten 2008).

Conclusions

Notwithstanding the need to look more closely at some of their ecological determinants, it seems likely that at least some of the candidates for traditional behaviors of chimpanzees as well as orangutans are indeed socially transmitted. But does that mean apes have culture in any meaningful way? On one view (e.g., Perry 2006), "cultural primatology" from the early study of Japanese macaques onward reveals a great deal about how culture evolves and what mechanisms maintain it. On another (e.g., Galef 2009), animal traditions are analogous but not homologous to human culture because the processes that perpetuate them do not include the key component of human cultural transmission, namely imitation. Human culture is indeed unique because across generations it "ratchets up": changes introduced in one generation are adopted and further elaborated in the next in a process of cumulative change. On one compelling account (Richerson and Boyd 2005), ratcheting up is possible because people are capable of exactly copying (i.e., imitating) behaviors of those around them and then improving on them by trial and error, reasoning, or other processes, whereas emulation and other social learning mechanisms leave each new generation to relearn much of what was learned by the last. On this view, although humans undoubtedly share some simpler social transmission mechanisms with other species, the propensity to imitate sets us apart even from chimpanzees (see Herrmann et al. 2007) and makes genuine culture possible.

13.6 Summary and conclusions

"Social learning" has a lot in common with "spatial learning" (Chapter 8). Both are essentially functional categories, that is, based on the kind of information acquired rather than on the way in which it is acquired, and both encompass a variety of specific mechanisms. However, individual mechanisms of spatial learning such as path integration, landmark use, and sun compass orientation are relatively well understood, whereas the analysis of separate mechanisms for social learning has been impeded by disproportionate interest in true imitation. The wave of recent research combining observations of naturalistic examples of social learning with experimental analyses of mechanism has led to an appreciation of how species-specific fine-tuning of simple learning mechanisms can lead to social transmission of adaptive behavior in natural social contexts. For example, rats learn about food by smelling other rats' breath because the smell of rat breath has motivational significance for them and because when rats greet each other the nose of one comes close to the mouth of another. A young black rat need never see another black rat stripping the scales off a pine cone; it needs only to be provided with cones than have been partially stripped in the right way (Terkel 1995).

Nonimitative social learning includes stimulus enhancement, observational conditioning, and emulation. None of these is very well understood in terms of the conditions that bring it about, the contents of that learning, and the effects of learning on behavior. Heyes (1994a) suggested that each is roughly analogous to a recognized category of associative or perceptual learning, but the questions she raised, such as the role of contingency and the possible occurrence of overshadowing and blocking in such learning, have still hardly been asked. It is necessary to answer them to know whether these kinds of social learning are distinctive in any way other than in the events that are learned about. There has, however, been considerable progress recently in understanding how imitation occurs and in what species, but emulation and affordance learning still need more study. In most circumstances there may be no need for strict imitation. The job can be done by emulation and the other social learning processes that don't require storing a representation of the demonstrator's behavior as such. Indeed, a tendency to blindly imitate what others do regardless of the positive or negative outcomes for oneself would likely be maladaptive. Thus what may need to be explained is not why most species seem incapable of true imitation but why any *are* capable of it. This explanation may ultimately have to do with the evolution of teaching and human culture.

Further readings

As illustrated in the first part of the chapter, the study of social learning has become exemplary as an area in which researchers from a whole range of different backgrounds—biologists, psychologists, and anthropologists, from mathematical modelers to field workers—are communicating and collaborating in rich and productive ways. Its development can be traced in books edited by Zentall and Galef (1988), Heyes and Galef (1996), and the February, 2004, special issue of *Learning & Behavior* (vol. 32, no.1). The chapter by Galef (1976) was influential in stimulating more recent developments and is still a valuable review of earlier work. The considerable work on social and other aspects of learning in dolphins is reviewed by Herman (2006). The many facets of the animal cultures debate are well represented in the book edited by Laland and Galef (2009). Bird song in all its aspects is reviewed in *Nature's Music* (Marler and Slabbekoorn 2004) and Zeigler and Marler (2004) and introduced more briefly in the book by Catchpole and Slater (1995). For teaching in animals, Caro and Hauser's (1992) review is recommended; the article by Hoppitt et al. (2008) is a brief overview of recent work.

14
Communication and Language

Figure 14.1 depicts a classic ethological example of communication. A male stickleback in breeding condition, with a red belly, swims in a wavering path toward an egg-laden female. When she responds to this "zig zig dance" by swimming toward the male, he heads toward his nest, and she follows. Upon reaching the nest, a little tunnel of vegetation on the substrate, the male pokes his head into the entrance, "showing" it to the female. She enters, and a further series of actions and reactions ends in her depositing eggs in the nest and the male releasing sperm over them.

Courtship in sticklebacks, as in most other animals, involves communication. Behaviors and structures apparently specially designed by natural selection are used by one animal to influence the behavior of others. In effect, the male's red belly and the zig zag dance tell the female something like "I am a male of your species, I have good genes and good health, I am ready to mate, and I want you to mate with me." But of course it is unnecessary to attribute such thoughts to the male.The courtship sequence can be understood as a chain of events in which one animal provides the stimulus for its partner's response, which in turn provides the stimulus for the next response in the chain, and so on.

Figure 14.2 depicts an account of what goes on when people communicate proposed by the philosopher Grice (1957). People generally assume they are modifying not only their listeners' behavior but their understanding. The young man in the figure is not just emitting sounds designed to cause the young woman to enter his car. Rather, he wants her to know that he is an attractive fellow who commands substantial resources and he would like her to come with him. On this view, human communication involves at least third-order intentionality (Section 12.3). In addition, it is referential. Unlike the stickleback's red belly, "Porsche" is not a stimulus that by itself attracts all sexually receptive females of the species. The man is referring to an object, and he intends to activate a representation of that object in his listener's mind.

A cartoon of stickleback behavior might have the male saying "I'm a fit and sexy male. Come with me and lay your eggs in my lovely nest," but few, if any, students of animal behavior would seriously consider a Gricean analysis of the stickleback's courtship. Traditionally, communicative behaviors such as displays or alarm calls were treated as expressions of emotion or motivation. More recently, some communicative behaviors have been interpreted as referring to objects in the world and as being given with intent to modify others' behavior, perhaps even their beliefs. Figure 14.3 depicts what is now a classic example. Vervet monkeys have three

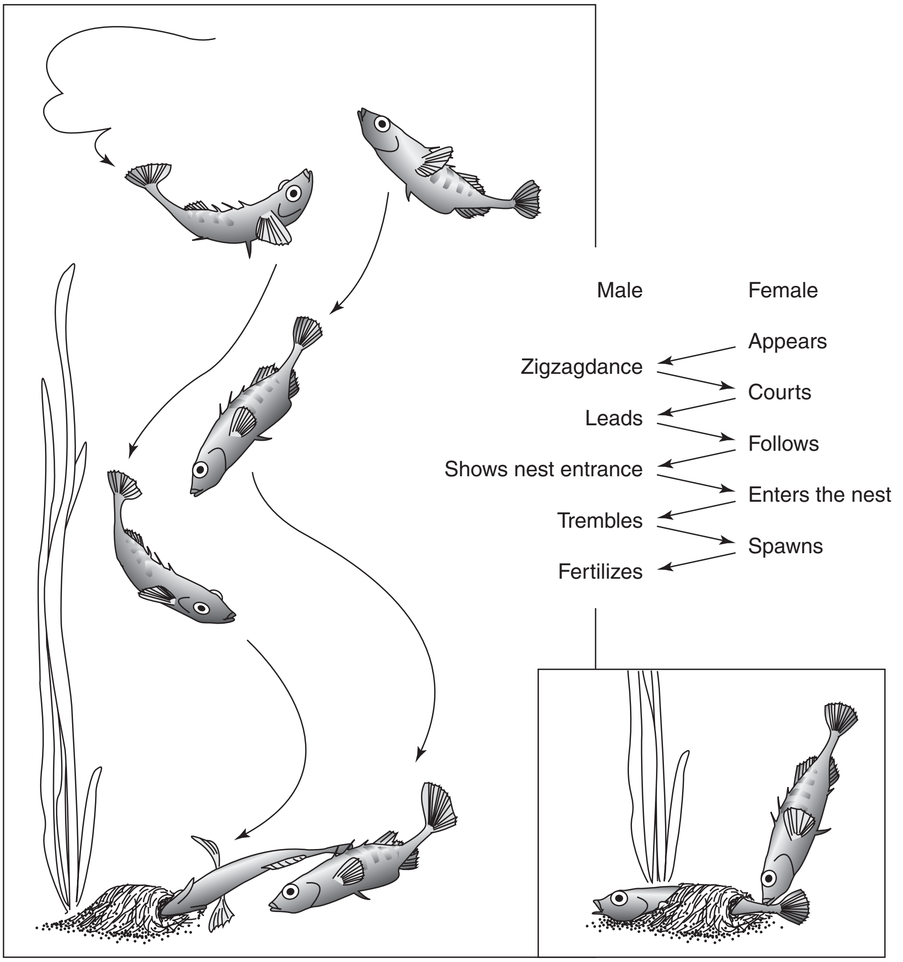


Figure 14.1. Courtship and spawning in the stickleback. After N. Tinbergen (1951) with permission.

acoustically distinct alarm calls (Seyfarth, Cheney, and Marler 1980). One is given to snakes. Vervets hearing it stand up on their hind legs and look at the ground. A second alarm call is given by a monkey sighting a leopard, and it causes nearby monkeys to run into the trees, out of reach of leopards. The third alarm call is given to aerial predators like eagles that can snatch monkeys out of trees. Vervets hearing it seek shelter at ground level. We could describe the vervets' communication as sequences of stimulus and response, as shown in Figure 14.3a, but would we be leaving out something important? Does an alarm calling vervet intend to modify other monkeys' behavior in definite ways or is he simply emitting a response to a predator stimulus? Do the three calls refer to three different predators? How could we tell? Exploring the possibility of reference and intentionality is an important thread in contemporary research on animal communication discussed further in Section 14.2.

As communications, the stickleback's approach to the female and the man's invitation to his date differ in another way than depicted in Figure 14.3. We would not be inclined to call the behavior sequence in Figure 14.1 *language* because the stickleback is limited to a small number of species-typical communicative acts put

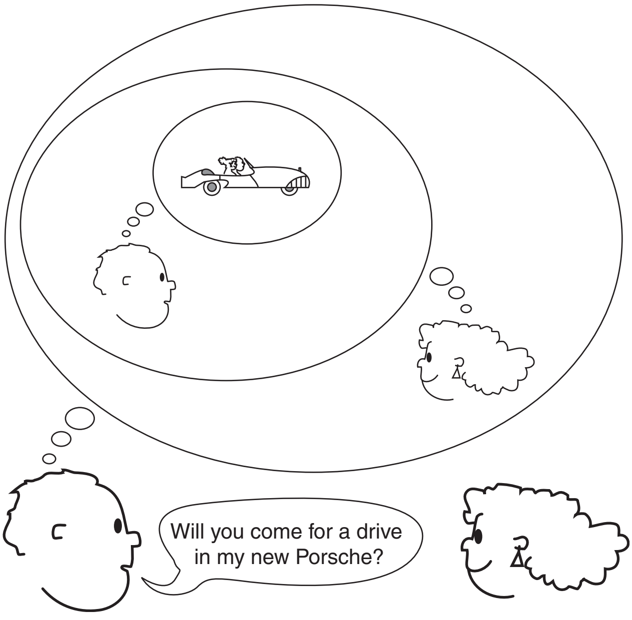


Figure 14.2. An example of human communication indicating the third order intentionality assumed to accompany it. Modified Gomez (1994) with permission.

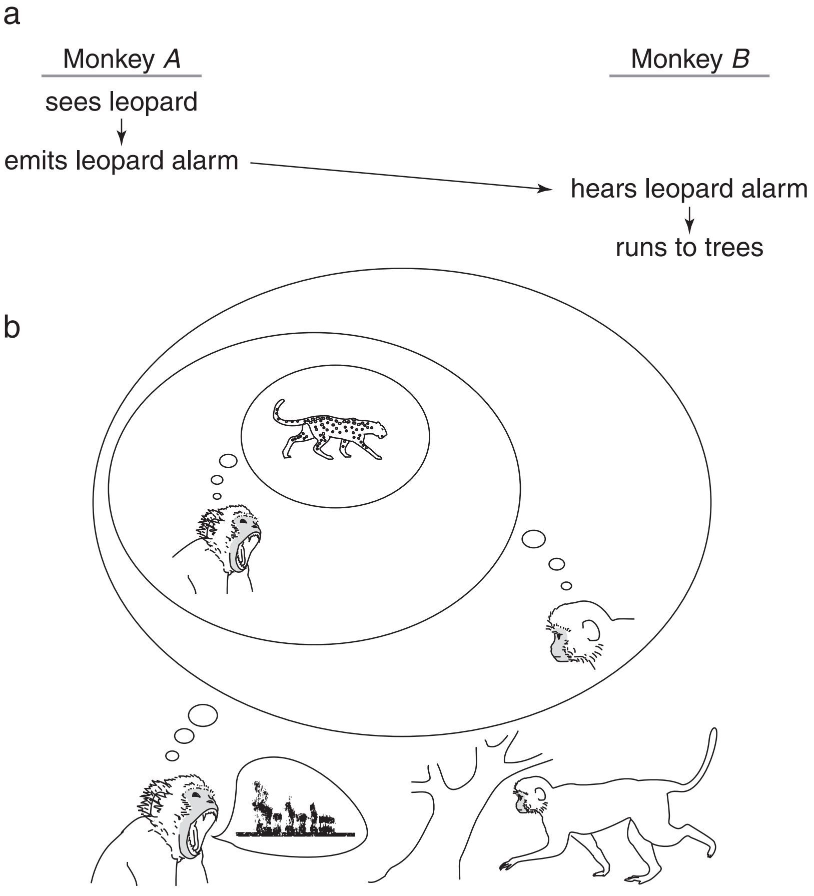


Figure 14.3. Two contrasting accounts of communication about predators by vervet monkeys. Vervets after Seyfarth and Cheney (1992) with permission.

together in a rigid way. Yet some animal communication systems, such as the dancing of honeybees, have been called languages. The vervets' alarm calls function somewhat like words. Discovering whether or in what way any animal communication systems share any properties of human language may help understand how human language evolved. The assumption that species phylogenetically closest to humans should have the most humanlike capacities for communication has inspired a long history of attempts to teach forms of human language to chimpanzees. The results of these efforts have implications for whether some aspects of language should be attributed to a cognitive module possessed only by humans. Section 14.3 reviews this research and Section14.4 expands on it with more recent developments in the study of language evolution. But first we consider a few general questions about animal communication (for more, see Maynard Smith and Harper 2003).

14.1 Some basic issues

14.1.1 Elements of communication

In communication, one animal influences the behavior of another through the transmission of *signals.* If my dog snarls and bares her teeth at your dog, she is signaling hostility. If your dog runs away because he sees my dog sleeping in the yard, we would be unlikely to say any signaling has taken place. But as we will see in a moment, the line between signaling and other kinds of information transmission is not always easy to draw. Classical ethologists studying communication focused on behavior patterns like the stickleback's zig zag dance that seemed selected specifically for a role in intraspecies interactions. Such behavior patterns are species-specific and occur in particular contexts. They also tend to be stereotyped in form, as in animals' characteristic submissive and aggressive postures (Figure 14.4). Figure 14.4 also illustrates what Darwin (1872/1965) in *The Expression of the Emotions in Man and Animals* called the Principle of Antithesis: signals with opposing meanings tend to be opposite in form. Signals may have evolved this way because antithesis reduces ambiguity. Recording the behavioral context for a candidate signaling behavior and other animals' responses to it are necessary for deciding what, if anything, is being communicated. Observations of freely behaving animals often lead to questions about

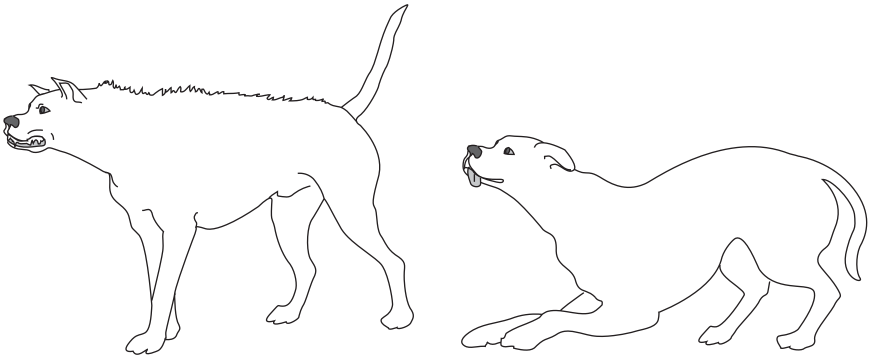


Figure 14.4. Contrast between aggressive and submissive postures, an example of the principle of antithesis. After Darwin (1872/1965).

communication that can best be answered with experiments. For instance, Tinbergen discovered which parts of the courtship sequence function as signals by using dummies, crude models with only some features of live fish (Figure 6.1).

Instances of communication involve not only a physical *signal* such as a sight, sound, or odor, but also a *sender* and a *receiver.* These terms all invite interpretation of animal communication as an active process, but animals may also transmit information about themselves in a more passive way. Red rainforest frogs or aposematic insects are spoken of as signaling that they are unpalatable, and indeed their bright colors and conspicuous patterns are thought to have been selected because predators easily learn to avoid such cues (Box 6.3). As another example, ragged fur, dull plumage, or the like function as signals of poor physical condition in that they may be perceived and responded to as such by potential mates or predators, but it seems unlikely they have been specifically selected as honest signals of quality. Similarly, as we saw in Chapter 12, even though animals that are being eavesdropped on during a social interaction are not specifically signaling to the eavesdropper, the eavesdropper may use their signals as cues for how to behave toward them in the future.

As we saw in Chapter 3, the physical properties of a signal and the receiver's perceptual sensitivity should be matched to each other and to the transmission properties of the environment. Thus a thorough analysis of animal communication integrates physics, ecology, sensory physiology and signal detection theory to explore why signals take the form they do (see Bradbury and Vehrencamp 1998; Owren and Rendall 2001; Wiley 2006). Depending on the species and situation, communication can take place through any of a number of channels, among them visual, olfactory, electrical, tactile, auditory. Here we focus almost entirely on auditory communication. Discussions of communication also consider the *messag*e of a signal and its *meaning* to the receiver (W. Smith 1977). The message is inferred from how the state of the sender and/or of the environment predicts what signal is given. For instance, does the species or proximity of predator predict the kind or intensity of alarm calling? The meaning of the signal, on the other hand, is inferred from the behavior of the receiver, so it may vary with the receiver's characteristics. For instance, in many species of birds, song is sung primarily by breeding males on their territories (Box 13.2). The song identifies the species of the singer, who he is, where he is, possibly something about his physical condition or the area he grew up in. These can all be considered part of its message. But the meaning of male territorial song is different for rival conspecific males (who may treat it as a challenge for a territorial fight or as a warning to stay away), conspecific females (who may treat it as a signal to approach), and birds of other species (who are likely to be indifferent to it).

14.1.2 The ethology and behavioral ecology of communication

The male stickleback's zig zag dance is a classic example of what ethologists call a *display,* a conspicuous stereotyped movement performed in a special context with an apparent communicative function. The zig zag dance is a example of a display arising from a motivational conflict, in this case between approaching the female and fleeing from her. *Intention movements,* the fragmentary beginnings of an activity that precede its full-blown appearance, are the other main evolutionary source of displays. The male's behavior of "showing the nest" is an example. In both cases, behaviors that normally occur in a given motivational context seem to have evolved into exaggerated and stereotyped, or *ritualized,* forms because exaggerated, stereotyped, displays are less ambiguous. Special coloration and patterning may also have been selected through making displays more noticeable to receivers (Chapter 3).

These ideas about the evolution of displays are supported by ethological studies from Lorenz (1941/1971) onward. Underlying many of them was the notion that communication is a matter of cooperation: signaling systems have evolved because both signaler and receiver benefit. Male and female sticklebacks can both increase their fitness by getting fertile eggs into the nest. The dog that growls and bares its teeth and the dog that runs away both avoid a potentially damaging fight. But ideas about individual selection imply that instead systems of animal communication evolve because animals benefit from manipulating one another (Maynard Smith and Harper 2003). No animal would be selected to give a costly display, one that takes time, consumes energy, and might increase its conspicuousness to predators, simply to share information with a conspecific. Signals must have been selected because they cause the receiver to behave in a way that increases the sender's inclusive fitness. The receiver, on this view, doesn't have to receive any benefit. At the same time, of course, the receiver's response to the signal, along with her perceptual sensitivity to it, will be selected only if it increases *her* net fitness. In contrast to the traditional ethological view, the view of communication stemming from emphasis on individual selection (Maynard Smith and Harper 2003) implies that signals are not necessarily truthful indicators of the sender's state. Instead signaler and receiver are engaged in an arms race. For instance, males may attract more mates and thereby increase their fitness by appearing to be bigger, stronger, and sexier than they really are. However, in species where fathers provide resources for their offspring, females will increase their fitness most by detecting the males that are truly healthy and good providers, since this will increase the chances that the bearers of their genes will be healthy and well provided for. The predator-prey interactions in mimicry systems (Chapter 6) are a case of deceptive interspecific signaling in that palatable prey sport the appearance of unpalatable ones. Here the evolutionary arms race is responsible for the very close resemblances between model and mimic, as well as between cryptic prey and background (Chapter 3). In some cases, however, honest signaling should evolve. For example, sexual selection favors signals like big tails and antlers because they handicap their owners (Zahavi 1975). A peacock that can keep himself in good condition and display vigorously to females in spite of producing and carrying around a huge tail can hardly be bluffing about his quality. Although the handicap principle and honest advertising were originally hotly debated, they are now generally accepted (see Maynard Smith and Harper 2003).

Receivers of signals can be thought of as engaged in "mindreading" (Krebs and Dawkins 1984) in that they may be able to tell what the sender of a signal will do next. For instance, the snarling dog is more likely to attack than to lie down. Mindreading in this sense means using the regularities in behavior in a predictive fashion. But whereas ethologists have to learn the predictive significance of other species' behavior patterns, the animals themselves may respond appropriately to signals like red bellies and territorial songs without much, if any, experience. Dawkins and Krebs's ideas about the evolution and function of communication stimulated a large amount of research and theorizing in behavioral ecology, as well as more than their share of controversy (Hinde 1981; M. Dawkins 1995). One point to take away is that terms like *mindreading, manipulation,* and *deception* do not imply that any animals are thinking about manipulating or deceiving each other any more than a grey moth resting on a grey tree trunk is thinking about deceiving hungry blue jays. They have clear functional meanings in the context of animal communication.

14.1.3 Language and animal communication

Whereas the biological study of animal communication traditionally focused on signals as indicators of the motivational state or behavioral propensity of the sender and on receivers' perception and response, a central issue in comparative cognition has been how nonhuman communication systems compare to human language. But all-or-nothing questions such as "Do any animals have language?" are not the best guides for comparative research. More worthwhile is to identify important features of human language and ask which, if any, of them are shared by the communication system of any other species and why. We look here at some of the components identified many years ago by Hockett (1960; for an update see Fitch 2005), which are still useful guides for comparing human language with the communication systems of other species. Notice that some (unbounded signal set, recursion) are formal characteristics of language whereas others such as reference imply mentalistic or representational skills.

Limited versus unbounded signal set

Most nonhuman species signal about only a few things—sex, aggression, predators, food—using a relatively small set of signals. Some signals are graded in intensity, corresponding for example to different levels of threat, but qualitatively different signals are rather few in number. In contrast, words—the elements of human language—and the ways in which they are put together make language essentially unbounded. *Outsourcing* and *email* are words invented in the 1990s as names for contemporary phenomena. More importantly, language is not just words but combinatorial principles, that is, rules for putting words together to devise new meanings. Therefore once we know what new words like *email* and *outsource* mean, we can immediately talk about them. For instance, we know that "Sue emailed John" and "John emailed Sue" mean two different things despite containing the same words. We also know that "Sue was emailed by John" means the same as "John emailed Sue," even though as a chain of visual or auditory stimuli it is more like "Sue emailed John." In general, animals do not combine their natural signals to create new meaning. In the rare exceptions the resulting signal does not seem logically related to the elements and their order. For example, male putty-nosed monkeys have distinct alarm calls and defensive behaviors for eagles and leopards, but occasionally when no predators are around they spontaneously give the two calls in sequence. These calls seem to predict upcoming initiation of movement by their family group (Arnold and Zuberbühler 2006).

Recursion

The unboundedness of language arises not so much from an ability to form unlimited numbers of associations between words and things or states of the world as from the ability to generate linguistic structure by *recursion* and to recognize and unpack the meaning of recursive structures. Formally, all but the simplest sentences are recursive in some way, that is they consist of patterns within patterns. As one straightforward example, the English sentence, "Jill remembered the time James said that I like cats that catch mice" embeds four subject-verb-object structures within one another, and it's easy to generate further embeddings. On one recently developed view (Hauser, Chomsky, and Fitch 2002), the implicit computational ability underlying recursion is the crucial component of human language not shared with any other species. This controversial (see Pinker and Jackendoff 2005) claim has stimulated attempts to test animals including starlings and tamarins for their ability to learn and discriminate recursive patterns. We look at these in Section 14.4.

Functional reference

In the examples earlier in the chapter, the male stickleback or the snarling dog are communicating that they are sexually aroused and aggressive, respectively. This information allows receivers to predict what the signaler will do next and behave appropriately. But as in Figure 14.2, people also use language to refer to objects and events in the world. The essential behavioral implications of reference are that, first, a signal that refers to a particular object or event is reliably given in its presence and not under other conditions. This criterion separates behavior patterns caused by generalized excitement or anxiety from those performed in the presence of specific arousing or dangerous conditions. Second, and equally important, the receiver of a referential signal behaves consistently in an appropriate manner, even in the absence of the object or event that elicited the signal. Thus an animal hearing a signal for flight flees whether or not it can hear or see something to flee from. Signals that meet these two criteria—*production specificity* on the part of the sender and *context independence* on the part of the receiver (Blumstein 1999)—are *functionally referential* (Evans 1997; Manser 2009). In what way, if any, a receiver's response to a functionally referential signal is mediated by a representation of the thing signaled is a further question discussed in Section 14.2.

Situational freedom (or *displacement*) is one concomitant of reference in human language. No food or danger need be present for us to talk about food or danger that we have experienced in the past or might experience in the future. As readers may suspect from the examples presented so far in this chapter, most animal signals do not exhibit situational freedom. The dance language of bees (Section 14.2.1) is sometimes cited as an exception. Besides allowing communication about objects and events in the past or future, situational freedom permits lying. Accordingly, one might ask whether animals can lie. This question refers not to the possibility that some signals are designed by evolution to deceive but to the cognitively more complex possibility that a signal with a particular message and meaning is occasionally used intentionally in another context for the sender's benefit. On the whole, there is little if any convincing evidence that animals lie, just as there is little evidence that they show other forms of intentional deception (Chapter 12).

Intention

Like the man in Figure 14.2, people generally use language with the intent of informing, changing the cognitive state of receivers. Behaviorally, this means suiting the communication to the audience: a professor gives different lectures to an introductory class and to a professional society. Further, what we say and how we say it are continuously modified by the perceived effects of our communication. If the students are baffled because they know nothing about evolution, the planned lecture on animal signals will be postponed, whereas if they reveal that they learned the basics of signaling systems in another course, the wise professor will move on to the next topic. The idea that animals might also communicate with intent to inform has been investigated in two ways. How the signaler's behavior is influenced by the other animals present, the so-called *audience effect,* has been analyzed in chickens, ground squirrels, and some primates, among other species. Whether signalers alter their behavior according to the response of receivers has also been looked at. On the whole such research has compared solitary signalers to those in a dyad, where the "audience" is the receiver. In principle audience effects might also be found when such a dyad is in the presence of onlookers or eavesdroppers, as in communication networks (P. McGregor 2005; Zuberbühler 2008). In either case, the underlying question is whether sophisticated conditional control by the behavior of receivers can be distinguished from control by the sender's understanding of whether the receivers are getting the intended message. The section on theory of mind in Chapter 12 suggests the answer.

14.2 Natural communication systems

14.2.1 Dancing honeybees

The waggle dance

People have been observing bees and collecting their honey since prehistoric times (Gould and Gould 1988). Aristotle noticed that when sugar water was set out to attract honeybees, no bees might arrive for several days, but once one did arrive others came soon after, apparently following the discoverer to the food. The mechanism underlying this recruitment was not elucidated until the first half of the twentieth century, when von Frisch and his students (von Frisch 1967) perfected methods for training bees to artificial food sources. The area of research opened up by von Frisch, and for which he was awarded a Nobel Prize together with Konrad Lorenz and Niko Tinbergen, is still flourishing (see F. Dyer 2002). Some of his conclusions, however, have had to survive a few challenges.

Von Frisch observed that when a bee returns from finding nectar 100 meters or more away, she may perform a *waggle dance* inside the dark hive on the vertical surface of the honeycomb. Bees returning from close to the hive perform a round dance. The waggle dance consists of a straight run in which the bee waggles her abdomen from side to side while vibrating her wings to make a buzzing sound. At the end of the straight run, she runs quickly back in a semicircle and begins another straight run. This return trip is made alternately to the left and to the right, tracing a figure-eight. Bees that have not recently been foraging successfully attend the dance, crowding around the forager and touching her with their anntennae. The waggle dance contains information about the distance and direction of the food source (Figure 14.5). The angle of the straight run to the vertical corresponds to the angle of the food source to the sun's current azimuth (see Box 8.2). If the food was located in a direct line from the hive toward the sun's azimuth, waggle runs will be oriented straight up on the vertical comb. If the sun is in the south and food is directly west of the hive, dances are oriented on average 90° to the right of vertical, and so on. The duration and length of the waggle run, together with the amount of buzzing accompanying it, corresponds to the distance to the food. The dancer also pauses from time to time and regurgitates a small drop of nectar, providing information about the kind of food. Whether dancing or not, the forager also carries odors from the food picked up by waxy hairs on her body. Finally, returning foragers that have found a resource needed by the colony are most likely to dance, and the vigor with which they dance corresponds to the value of the resource. Bees dance not only after gathering nectar but also after finding pollen, water, tree sap, and potential new nest sites (Seeley 1995).

The waggle dance clearly carries information, but do other bees use it? The designs von Frisch used for testing use of direction and distance information, respectively, are depicted in Figure 14.6. Marked foragers are trained to come to a feeding platform that is gradually moved further and further from the hive. Because they are offered a

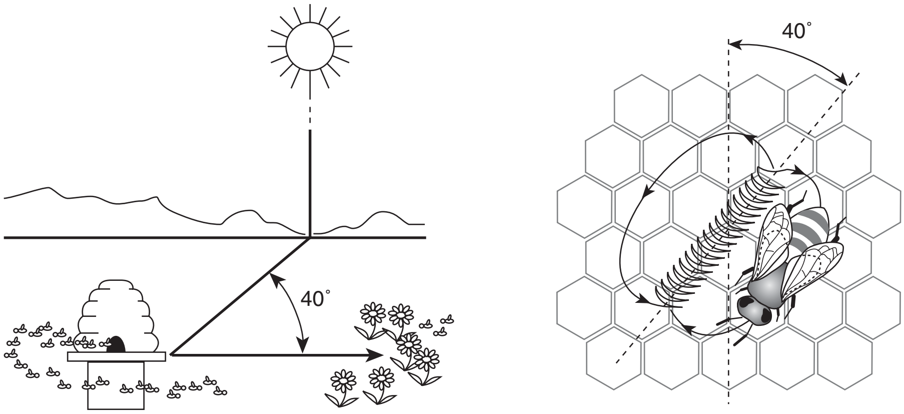


Figure 14.5. The waggle dance of the honeybee showing how its angle to the vertical is related to the angle between the path to the food and the sun's azimuth. Redrawn from Seeley (1985) with permission.

relatively weak sugar solution at this stage, they do not yet dance and recruit other bees. On the test day, the solution is made strong enough to elicit dancing, control platforms are set out along with the training platform, and arriving bees are counted at each one. In the "fan experiment," to test the use of directional information the control feeders were all equidistant from the hive, spread out on both sides of the training feeder. In the "step experiment," to test for the use of distance information the control feeders and the training feeder were in the same straight line from the hive, with control feeders both nearer and farther than the training feeder. In both cases, the majority of recruits turned up at the training location.

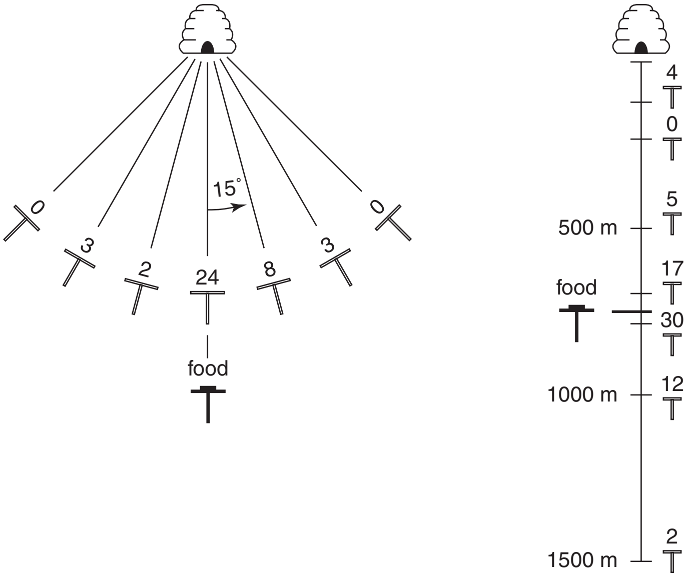


Figure 14.6. Arrangements of training ("food") and control feeders in von Frisch's "fan"(left) and "step" experiments, showing the number of bees arriving at each one in the test. Fan redrawn from von Frisch (1953); step based on data in von Frisch (1967).

The dance language controversy

At first glance, the results of the “fan” and “step” experiments seem clear evidence that recruits use the information in the dance. However, a few cautions are necessary. Recruits are generally much slower to arrive than experienced foragers, and not all the bees attending a dance necessarily find the indicated site. Furthermore, long before he discovered the waggle dance, von Frisch established that bees can find sites recently visited by other bees by odor alone. They use not only the odor of the food itself (e.g., from a flower), but other odors at or near the site including odors deposited by successful foragers. In the late 1960s the clear importance of odor together with the results of some experiments similar but not identical in detail to von Frisch’s fan and step experiments led Wenner and others to reexamine the dance language hypothesis (Gould 1976; Wenner and Wells 1990). They concluded that the dance did not function as communication. All von Frisch’s results, together with the results of their new experiments, could be explained by the bees’ use of odor. In both the fan and the step designs, the target feeder, the one where most bees turn up, is the center of a gradient of odor from the whole array of feeders. In addition, it is the location that has been most visited by bees. When arrays had the target feeder offset from the center and controls were instituted for past bee visits, most recruits still turned up in the center of the array rather than at the feeder signaled by the dancers.

Wenner’s attack on the dance language hypothesis was answered by von Frisch himself among others (see Gould and Gould 1988), and in the early 1970s the question of whether or not the waggle dance was communication was *the* controversial issue in ethology. Most biologists now regard it as settled (F. Dyer 2002). Three new kinds of experiments show conclusively that bees use the information in the dance even if, as described at the end of this section, they do not always do so. The first relevant experiment has a simple logic that we meet again in considering referential communication in other species: if a signal functions to communicate, then receivers must respond appropriately to it even in the absence of the environmental conditions that gave rise to it. Otherwise it is impossible to be sure whether they have responded to the signal or directly to the state of the environment. James Gould, then a graduate student, saw that this could be accomplished for the bees’ dance by dissociating the direction signaled by dancers from the direction to the food (Gould 1975). In effect, he caused dancing bees to lie and other bees to believe them. He did this by making use of the fact that although bees in the dark orient and interpret dances with respect to the vertical, bees in the light use the sun. For instance, in the dark a dance elicited by food 90° to the right of the sun’s azimuth will have a straight run 90° to the right of vertical, but in a lighted hive dancers arriving from the same place will orient 90° to the right of the light. Gould further made use of the fact that bees perceive the overall level of illumination with their ocelli, an array of photoreceptors on the top of the head. Bees whose ocelli are covered with opaque paint behave as if in dim light. Most importantly, at some levels of hive illumination untreated bees reorient their dances and their interpretation of dances to the light while bees with painted ocelli do not. What Gould did was to train some foragers with painted ocelli to a target feeder and cause them to dance in a lighted hive where the attendant bees had unpainted ocelli. The dance was oriented with respect to gravity while the potential recruits interpreted it with respect to the light. In this way Gould dissociated the location actually visited by the dancers, which recruits might have detected via odor, and the location indicated by the dance. Contrary to the odor hypothesis but consistent with the dance language hypothesis, most recruits arrived at the feeder indicated by the dance.

A second experimental approach to testing whether dancing communicates distance and direction employed a traditional ethological tool for presenting signals independently of the environmental conditions that normally elicit them, namely a dummy, here a mechanical bee. A mechanical bee successfully recruits bees that attend its dances, and the recruits use both distance and direction information provided by the model (Michelsen et al. 1992). An even newer technical development has provided a third kind of evidence for use of dance information. Bees that had attended a dance were fitted with transponders for harmonic radar as they left the hive, so their flight paths could be recorded (see Section 8.4.2; Riley et al. 2005). Whether they were released at the hive or at other locations 200 meters away, the recruits flew for roughly the correct distance in the direction indicated by the dance. Then they began to circle around as if searching for other cues to the food's location (Figure 14.7). Odor is normally one such cue, as discussed more below, but the feeders in this experiment were all unscented.

Not only does the experiment of Riley and colleagues (2005) provide direct evidence that the bees, in effect, treat the dance as flying instructions ("go this far in this direction"), it also provides evidence against suggestions that recruits' cognitive maps of the local environment mediate their responses to it. If the bees displaced as indicated in Figure 14.7 had interpreted the dance as telling them about a certain allocentrically defined location, they should have headed toward it rather than directly east and they should have flown farther in that direction before starting to search for the feeder. However, under some conditions experienced bees' maplike knowledge of the local terrain seems to influence how they dance and respond to dances (Section 8.4.2; R. Menzel and De Marco 2006), and a long-standing but sketchily reported experiment is said to indicate the same. This is the "lake experiment" (Gould and Towne 1987; Gould 1990), in which recruits reportedly did not follow dances telling them food was in the middle of a lake, a location in which food was normally very unlikely (the dancers having been trained to a feeder on a boat

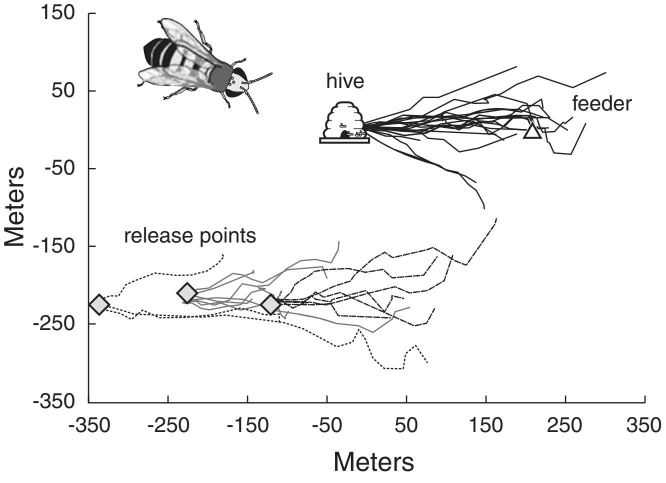


Figure 14.7. Flight paths of honeybees recruited by dancers that had visited the feeder shown (triangle). Some set out from the hive (coordinates 0, 0), and others were released at distant locations (diamonds). Paths were recorded until the bees began to circle around as if searching for cues from the feeder. After Riley et al. (2005) with permission.

which was slowly moved to the middle of the lake). A thorough recent repetition of this study (Wray et al. 2008) provided no evidence that the recruits were mentally traveling to the location signaled by a dance and refusing to follow directions that would take them to the implausible lake.

But exactly what spatial information is encoded in the dance? Foragers forced to follow an indirect route to food, for example around a mountain, seem to "report" the straight line direction to the food, as if using path integration to record the journey (von Frisch 1967; F. Dyer 2002; R. Menzel and De Marco 2006). As for distance, we saw in Box 8.3 that bees measure distance by optic flow. This subjective distance is what the dance communicates. Foragers that have found food in a densely patterned tunnel dance as if food is farther away than it really is, and that is the distance flown by recruits heading out across natural terrain (Esch et al. 2001).

One aspect of local knowledge that does influence recruits' behavior is what they know about the odor carried by the dancer. Although odor does not have the role attributed to it by skeptics who claimed it was the only information imparted in the dance, bees do use it. We have already seen a suggestion (Riley et al. 2005) that when new recruits have flown the vector encoded in the dance to the approximate location of the food, they find the feeder itself using local cues. Normally those would include an odor matching that on the dancer. Experienced bees remember the odor as well as the color of food sources at specific locations. If a familiar location has been without food for a few hours (so bees stop visiting it) and its odor is simply blown into the hive, bees start flying out to visit it (Reinhard et al. 2004). This is evidently a naturalistic example of memory reactivation (Section 7.5). Bees can hold two such odor-location associations in memory at once. They also associate color with odor. When yellow rose-scented and blue lemon-scented feeders were experienced at a variety of locations equidistant from the hive and rose odor was wafted into the hive, the bees selectively visited yellow sites even though they were unscented in the test (Experiment 5 in Reinhard et al. 2004). Such stored personal information may even be used in preference to conflicting public information from a dancer (Grüter, Balbuena, and Farina 2008). For example, if a dancer carries an odor that an experienced but currently inactive forager associates with location A but the dancer is signaling novel location B, in a different direction, the forager will visit A rather than B. The spatial information in the dance may primarily be used by naive bees just beginning to forage or those that have not been foraging recently, whereas the dancer's odor or even its dancing alone serves to reactivate experienced foragers, which then visit sites they already know (Grüter, Balbuena, and Farina 2008).

Conclusions

The dancing of bees differs from the communication systems to be discussed next in that a continuously graded message signals a potentially infinite number of directions and distances. The dance has also (e.g., Roitblat 1987) been claimed to be unique among animal communications in having the human-language property of displacement. This is obviously true in a trivial sense, since the dancer may be displaced in space several hundred meters from the food that caused her to dance. However, if the dance is seen as reporting on a just-completed journey, it is no more displaced than an alarm call given to a just-glimpsed snake. In both cases, too, the communication is symbolic in that the signal bears an arbitrary relationship to the message. It has been suggested that "the dance-communication system of honey bees . . . is exceeded in complexity and information-carrying capacity only by human speech" (Gould and

Towne 1987, 317–318). This conclusion may be overenthusiastic, but there seems no reason to question von Frisch's assertion (see F. Dyer 2002) that the study of the honeybees' dance is a "magic well of scientific discovery" and much is still being drawn from it.

14.2.2 Chickens: Audience effects, functional reference, and representation

Chickens have two kinds of alarm calls (Figure 14.8). Aerial predators such as hawks elicit a scream or whistle, whereas ground predators such as foxes and raccoons elicit a long series of pulses, "cut cut cut cut . . . cuuut." Behavior toward these two classes of predators differs in a functionally sensible way. A chicken sighting a hawk overhead may move toward cover, and it crouches and repeatedly tilts its head to one side, looking up at the sky. When a fox, dog, or raccoon approaches, the chicken stands erect and looks from side to side.

Chickens' alarm calls satisfy the criteria for functional reference. Roosters were presented with video images of either a hawk on an overhead monitor or a raccoon on a monitor at the side of their cage (Figure 14.9). They gave aerial alarm calls to the hawk and ground alarm calls to the raccoon and otherwise behaved appropriately to each one, thus showing production specificity (Evans, Evans, and Marler 1993). The context independence of responses to alarm calling was shown by playing recorded alarm calls to hens isolated in a laboratory cage. The hens moved toward cover only when hearing an aerial alarm, and they crouched and looked up most often in this condition (Figure 14.8). Hens hearing ground alarms did not seek cover, crouch or look up any more than hens hearing background noise. Instead they stood in a tall sleeked posture and looked from side to side. Unlike in the risk-based systems to be discussed in Section 14.2.5, the differences in behavior to aerial and ground predators do not reflect quantitative differences in the threat posed by the predator. For instance, the number

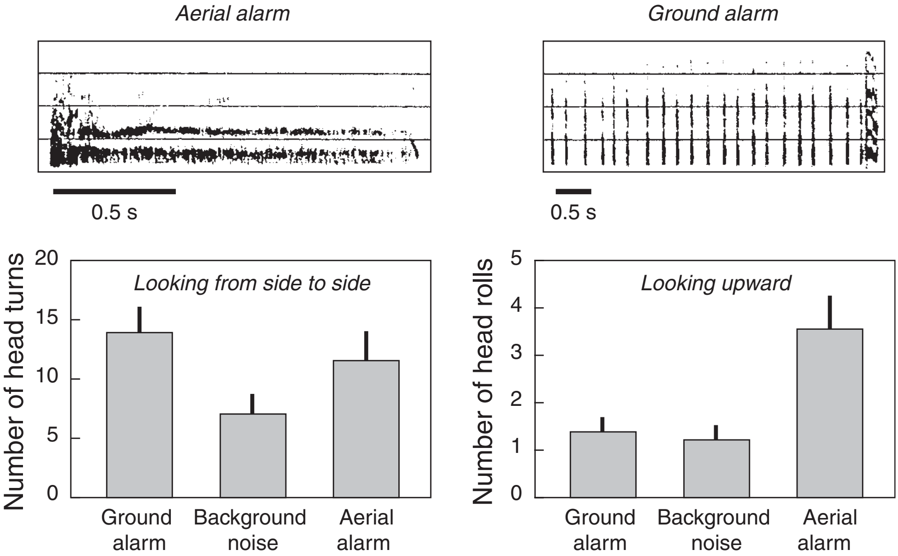


Figure 14.8. Sonagrams and behavioral effects of chickens' aerial and ground alarm calls, compared to effects of background noise. Redrawn from Evans, Evans, and Marler (1993) with permission.

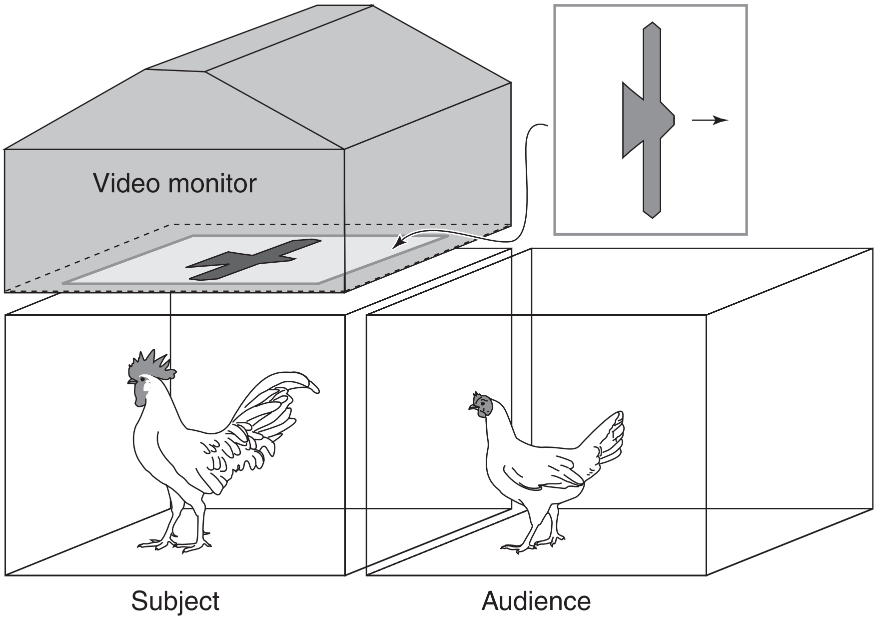


Figure 14.9. Setup for studying effects of the presence of a hen (the audience) on a rooster's alarm calling. Redrawn from Evans and Marler (1992) and Evans, Macedonia and Marler (1993) with permission.

of alarm calls and nonvocal responses increased with the size of an overhead hawk image, but their nature remained the same (Evans, Macedonia, and Marler 1993).

Alarm calling makes sense only if other animals are around to get the message. Indeed, by attracting a predator's attention calling may be costly for a solitary animal. Operationally this means that alarm calling should be modulated by the presence versus absence of an audience. Roosters alarm call more when they can see a live or videotaped hen (Evans and Marler 1995). The characteristics of the audience are also important: roosters alarm call more when the audience is a conspecific than when it is a bobwhite quail (Karakashian, Gyger, and Marler 1988). Notice that the results of these experiments do not demand an intentional interpretation. What is being shown is that aerial alarm calling is affected by characteristics of both the predator and the audience.

Roosters' food calling is also sensitive to the audience. When hens are around, a rooster finding a morsel of food emits a food call and hens are attracted to it, are allowed to eat it, and may subsequently engage in other aspects of courtship with the rooster (Marler, Dufty, and Pickert 1986a, 1986b; Evans and Marler 1994). Here again is a behavior that invites interpretation in terms of intentions to communicate, to attract the hen, and so on, but again it is more simply characterized as conditionally controlled by, among other things, the quality of food and kind of audience. Food calling is also functionally referential (Evans and Evans 1999). Roosters food call not only when they find food in the presence of an audience, but also in the presence of a CS for food; thus in a sense their calls express an expectation of food (Evans and Marler 1994).

On the receiver's side, when a hen hears a food call, but not a ground alarm call, she closely scans the ground as if looking for food. To discover whether she does so because the call represents food, as opposed to eliciting scanning directly, Evans and

Evans (2007) adopted the logic of experiments designed to test whether conditioned responses result from S-S or S-R learning. As described in Chapter 4, such experiments may involve manipulations like devaluing food by poisoning or satiation, to, in effect, change the animal's representation of the US directly without altering the original CS-reinforcer (S-S) or CS-response (S-R) connections. If responding to a CS is mediated by a food representation, that is, if it reflects CS-food rather than CS-response learning, responding decreases immediately when food is devalued. Evans and Evans (2007) reasoned that, similarly, if the hen's response to food calling is mediated by a representation of food, prior information that food is present should decrease it. This prediction was borne out. When hens had recently found and eaten three corn kernels in the experimental chamber, they scanned the ground in response to a food call much less than hens that had not just found corn and no more than hens that heard a ground alarm. Because so little food was given, the hens' lack of responsiveness most likely reflected not satiation but rather the fact that the call gave no new information.

14.2.3 Vervet monkeys: Categorization and intentional communication

In effect, the vervet monkeys' three alarm calls—for eagles and other dangerous raptors, snakes, and leopards (Section 14.1; Figure 14.10)—show how vervets classify predators in much the same way as a pigeon's pecking a different one of four keys in the presence of pictures of different kinds of objects shows how the pigeon is classifying the images (Chapter 6). Vervets make finer discriminations among flying things than chickens do (Figure 14.11). Chickens living outdoors in rural New York State gave a high proportion of their aerial alarms to harmless birds like doves and geese, and even to airplanes and falling leaves, but adult vervets discriminate potentially harmful raptors (hawks and eagles) from equally large but harmless birds such as storks and vultures. This discrimination develops during the first four years or so of life (Seyfarth and Cheney 1986). Infant vervets give the three types of alarms calls in a roughly appropriate manner, for example, eagle alarms to things in the air and snake alarms to long things on the ground. But at first infants do not show much discrimination among things within these classes. For instance, eagle alarms are as likely to nonraptors as to raptors. When juveniles begin to discriminate between the broad

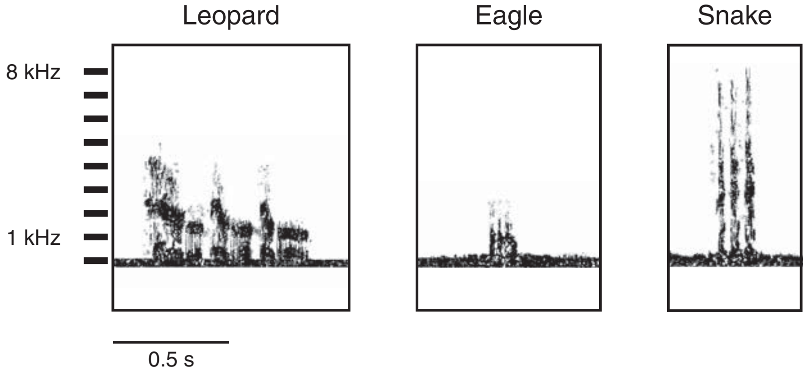


Figure 14.10. Sonagrams of one individual vervet's leopard, eagle, and snake alarms. From Seyfarth, Cheney, and Marler (1980) with permission.

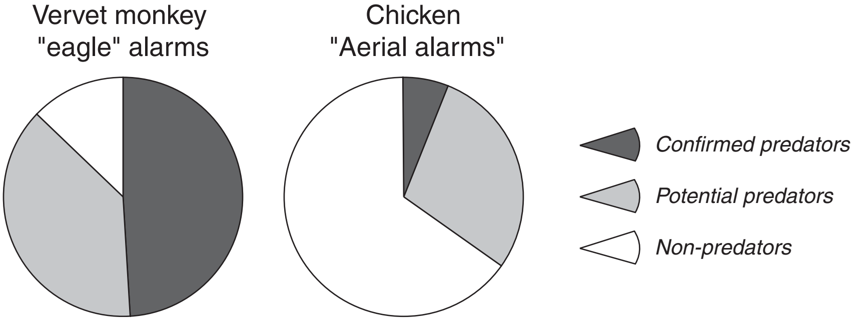


Figure 14.11. Comparison of the specificity of vervet eagle alarms and chicken aerial alarms, in terms of the proportions of calls given to confirmed predators versus other aerial things. Redrawn from Evans and Marler (1995) with permission.

classes of raptors (hawks and eagles) versus nonraptors, they still include raptors that do not prey on monkeys, but later these are more or less ignored. Because these developmental changes take several years, it is impossible to say exactly what experiences contribute to them and how they do so, but teaching by older vervets does not appear to be involved (Cheney and Seyfarth 1990). Adults do not, for example, correct infants when they call inappropriately. Observational learning similar to birds' and other monkeys' observational learning about predators (Chapter 13) may play a role.

The vervets' categorization of predators makes functional sense because each one demands a different response. Eagles strike from above, so monkeys that are high in trees when an eagle is sighted should move down while monkeys on the ground should move into cover. Leopards, in contrast, generally attack monkeys on the ground and can be escaped by climbing trees. Snakes approach along the ground and may be mobbed by the monkey troop. In opportunistic observations in the field, animals' responses to others' calls may be hard to distinguish from responses caused by their own sighting of the predator or other animals' behavior to it, but alarms by themselves elicit appropriate responses when played from concealed loudspeakers in the absence of predators (Seyfarth., Cheney, and Marler 1980).

Vervet alarm calls meet the criteria for functional reference, but do they simply elicit predator-appropriate responses or do they access a representation of a particular type of predator? And since different individuals have different voices, is something about the caller represented as well? To try to find out, Cheney and Seyfarth (1988) turned to habituation-dishabituation experiments. Some of them focused not on alarm calls but on vocalizations used in intergroup encounter. *Wrr*s are emitted when another group is approaching, as are *chutters,* but chutters are more frequent in direct aggressive interactions between groups. Because vervets tend to look toward a calling animal, Cheney and Seyfarth counted the number of seconds looking toward the speaker in films of the period during and immediately after playbacks. Each experiment began with a playback of the target call to get a baseline measure of orienting. On the next day, the subject heard a series of eight habituating calls about 30 minutes apart, during which looking time generally declined. About 30 minutes later, the target call was played again and looking time was compared to baseline (Figure 14.12).

This design was used to test whether habituation transferred from wrrs to an acoustically different call with similar meaning, chutters, and whether the identity

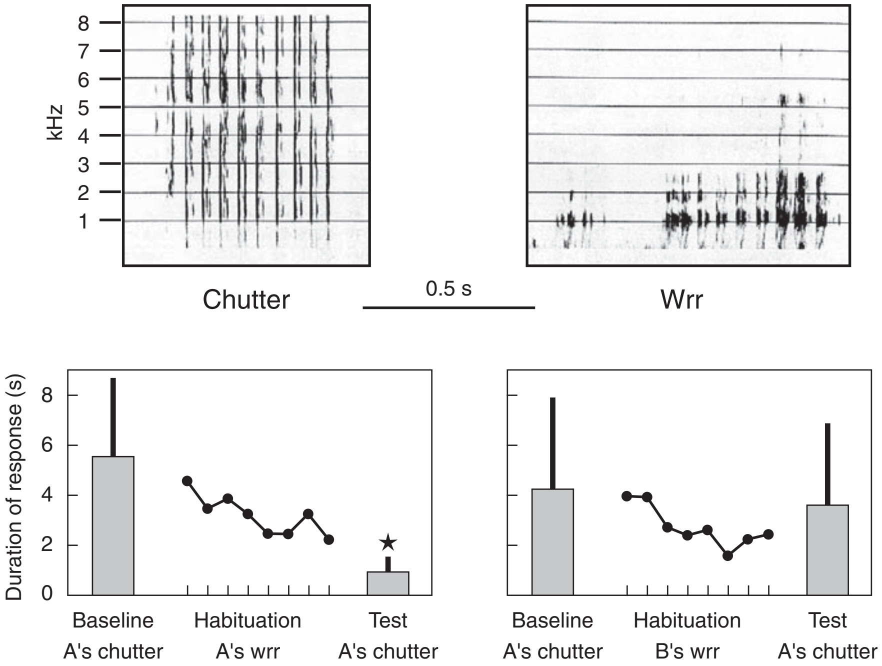


Figure 14.12. Sonagrams of wrr and chutter vocalizations of a single individual and data demonstrating cross habituation between two calls from the same caller. Redrawn from Cheney and Seyfarth (1988) with permission.

of the caller mattered to any transfer of habituation. In effect this design asked, if animal A was unreliable because he repeatedly wrr'd from the bushes and no vervet group appeared, would he be treated as unreliable when he chuttered? A second series of tests asked whether an animal habituated to an eagle alarm would transfer this habituation to leopard alarms, and, again, would it matter if the same or different individuals gave the two kinds of alarms? Regardless of the identity of the caller, habituation did not transfer between eagle and leopard alarms, nor did it transfer from one individual's wrr to another's chutter. However, habituation did transfer from a given individual's wrrs to that same individual's chutters, as if the vervets learned something like "Charlie is unreliable today when it comes to signaling the approach of another group." Because transfer was obtained here but not when the same individual was heard to signal two different predators, it appears that habituation transfers between two acoustically different calls only if they have similar meaning. However, one might still worry that in some sense a wrr and a chutter from a single individual are more similar to each other as acoustic stimuli than are an eagle and a leopard alarm from one individual. But this doubt is laid to rest by evidence that habituation can transfer across acoustically very different calls—a bird's and a monkey's predator alarms (Seyfarth and Cheney 1990).

Superb starlings (*Spreo superbus*) live with the vervets in Kenya and give acoustically distinctive "raptor alarms" to birds that attack them from the air. The starlings also give "terrestrial predator" alarms to a wide variety of ground predators. Vervets respond to both of the starlings' alarm calls, apparently learning to do so (Hauser 1988). As would be expected if the vervets are responding in terms of what the calls signal, habituation transferred between vervet and starling raptor alarms, whereas it did not transfer between vervet leopard alarms and starling raptor alarms. The starling raptor alarm is elicited by aerial predators, not by leopards. However, habituation to the much less specific starling terrestrial predator alarm transferred to both vervet leopard alarms and vervet eagle alarms. As Seyfarth and Cheney concluded from the results of their playback experiments (1990, 764), "The results of these tests are difficult to explain without assuming that vervets have some representation of the objects and events denoted by different call types, and that they compare and respond to vocalizations on the basis of these representations." What is being described here and even more so in the next section is much like many-to-one matching or mediated generalization (Chapter 6), in which arbitrary conditioned stimuli are related to one another via an association with a common US or response. Indeed, Seyfarth and Cheney (e.g., 1997, 2003c) have emphasized that many of their findings are consistent with explanations in terms of associative learning. In any case, as with most observations that meet the criteria for functional reference, we cannot tell exactly what the calls refer to (Manser 2009). A leopard alarm, for instance, could equally well denote a leopard or be an imperative, "run to the trees if you're on the ground and stay in the trees if you're there already."

Whatever the conclusion about the meaning of signals, it is a different question whether they are used with intent to inform. Like chickens, alarm calling vervets show an audience effect. A solitary vervet is unlikely to alarm call. However, there is no indication that an alarm calling vervet takes into account the audience's need to know. The individual that first discovers the snake or the leopard should be more likely to call than one whose fellows are already calling or safe from predation, but extensive observations of vervets in the field yielded no evidence for this (Cheney and Seyfarth 1990). Research on baboons' contact barks (Cheney, Seyfarth, and Palombit 1996) and reconciliatory grunts (Cheney and Seyfarth 1997) leads to the same conclusion (Cheney and Seyfarth 2007). For example, baboons that have become separated from their troop emit "contact barks" but troop members within earshot do not vocalize in response as they should if they understand that the barking animal is trying to locate the group. The evidence relevant to intentional communication in vervets and baboons can thus be summarized as showing that while callers are sensitive to some properties of their audience, they do not take other animals' understanding into account (for review see Seyfarth and Cheney 2003c). This conclusion is of course consistent with the indications in Chapter 12 that monkeys do not have theory of mind.

14.2.4 Diana monkeys: understanding other species' signals

Diana monkeys (*Cercopithecus diana diana*) live in the rainforests of West Africa in groups consisting of a male with several females and their offspring. Male Diana monkeys make acoustically distinct alarm calls in response to leopards, which attack these arboreal monkeys from below, and crowned eagles, which snatch them from above. In the forest it is impossible to observe everything the monkeys do in response to signs of a predator, but because female Diana monkeys respond to male eagle and leopard alarms by calling in characteristic ways themselves, females' vocalizations provide insights into how the monkeys classify sounds from their own and other species. For example, females' calling habituates if the same male alarm call is repeated, but if a series of, say, leopard alarms is followed by an eagle alarm, females call anew in response to the call signifying a new kind of threat. The alarm calls are functionally referential in that they have both production specificity and context independence (Zuberbühler 2003).

Further evidence for functional reference comes from elegant experiments based on the fact that females call appropriately in response to vocalizations of the predators themselves. Zuberbühler, Cheney, and Seyfarth (1999) compared females' responses to an eagle's shriek (a probe stimulus) following each of three habituating experiences (or *primes*): a series of eagle shrieks, a series of male eagle alarms, and a series of male leopard alarms (Figure 14.13). "Eagle" alarm calling to the eagle probe remained at a low level in the first condition, whereas it was high when the females had just heard a series of leopard alarms. In the critical condition, eagle shriek following eagle alarms, calling also remained low, a result that could be described as showing that the females expected to hear an eagle when the male had just "told" them one was around. Analogous results were found with leopard growls as the probe following habituation to eagle alarms, leopard alarms, and leopard growls.

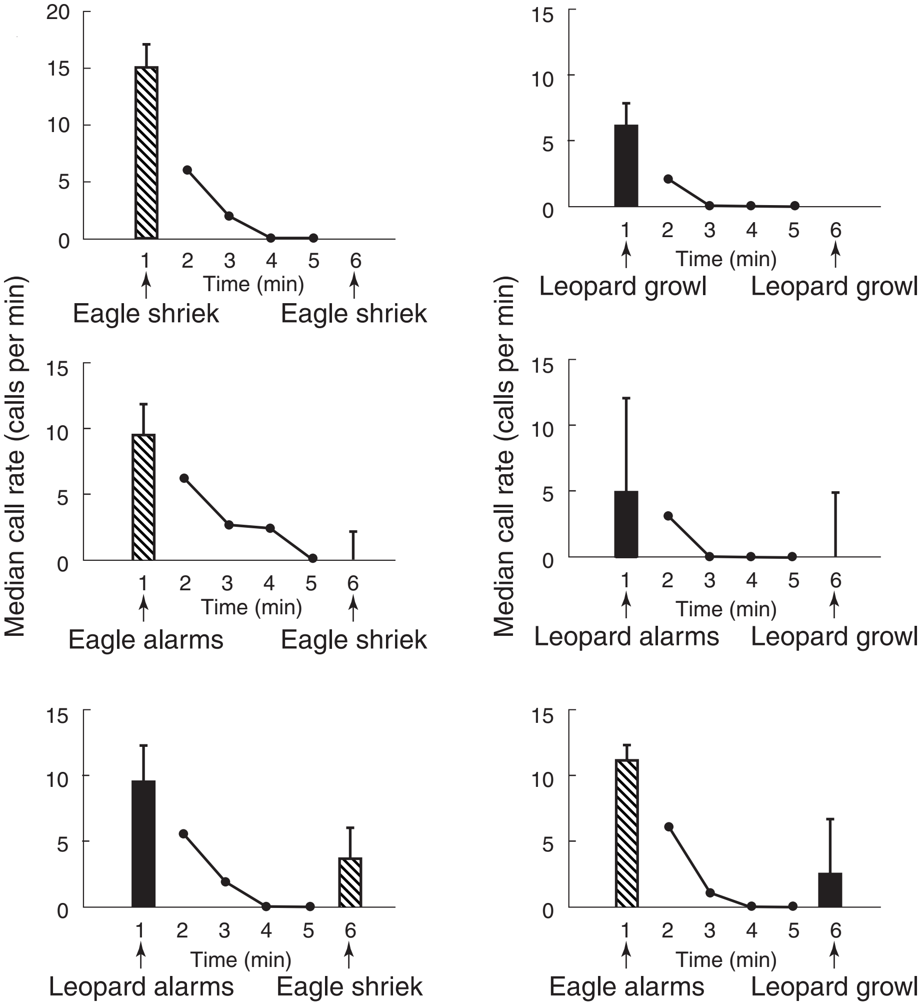


Figure 14.13. Calling of female Diana monkeys to a probe of an eagle shriek (left column) or a leopard growl following habituation to a prime consisting of the same stimulus (e.g., eagle shriek), or male diana monkey alarm calls given to the same predator (e.g., eagle alarm), or a different predator (e.g., leopard alarm). After Zuberbuhler, Cheney, and Seyfarth (1999) with permission.

Notice that with this experimental design the effect of a standardized probe such as the eagle's shriek in Figure 14.13 is compared across groups of subjects that have had different priming stimuli. This is more powerful than simply measuring response to a call before and after habituation as in some related experiments because it controls for the possibility that general responsiveness changes during the habituation treatment (Evans 1997). Much as with Wagner's model of memory (Chapter 5), the results imply that the leopard's growl and the leopard alarm access a common representation because exposure to either one decreases responsiveness to the same probe. In this sense the monkeys represent or remember some correlate of the specific predator signaled (Seyfarth and Cheney 2003c).

Not only primates but birds (Rainey, Zuberbühler, and Slater 2004; Templeton and Greene 2007) and even a reptile, the Galapagos iguana (Vitousek et al. 2007) learn to respond to the alarm calls of sympatric species. Diana monkeys learn some quite subtle things about the vocalizations of other animals they commonly encounter (Zuberbühler 2003). For example, leopards hunt chimpanzees as well as monkeys, and diana monkeys that frequently contact chimpanzees (but not those which do not) make leopard alarms when they hear chimpanzee alarm screams, as if having associated the chimpanzee screams with the presence of a leopard. But diana monkeys are also hunted by chimpanzees, and their response to signs of predatory chimpanzees or humans is not to alarm call but to be silent and cryptic. Accordingly, this is how they behave when they hear chimpanzee social screams or human voices (Zuberbühler 2000b). They learn even more subtle discriminations involving the alarm calls of crested guinea fowl, a species preyed upon by—and giving the same alarm call to—both leopards and humans (Zuberbühler 2000a). By themselves, guinea fowl alarm calls evoke leopard alarms from diana monkeys. But the monkeys call at only a low level if they have been primed with the sound of human voices, as if inferring that humans rather than leopards had caused the guinea fowls' alarms. In contrast, when priming with human voices is followed by the growl of a leopard, they do make leopard alarm calls, showing that signs of people in the area do not evoke cryptic behavior in general.

These findings can be described as showing the monkeys are making causal inferences. They might even fit one of the causal models discussed in Section 11.3.3. However, the monkeys' causal knowledge need not go beyond that implicit in simple associative learning (Zuberbühler 2000a, 2000b). For example, diana monkeys may respond to signs of a leopard by approaching in a group to keep an eye on it from a safe distance. Thus they could well have witnessed encounters between leopards and chimpanzees; even if rare these would provide the conditions for associating chimpanzee alarm screams with the presence of a leopard. Similarly, the way in which the monkeys' response to guinea fowl alarms is conditional on the context could have developed through experiences analogous to those required for occasion setting (Section 4.6). More evidence about the animals' prior experience than can readily be collected in the rainforest would be necessary to test such accounts. A further question is what any of these observations imply about the calls' reference. Different sounds such as leopard growls and alarm calls of monkeys, chimpanzees, and guinea fowl are evidently functionally equivalent (see Chapter 6). Whether the behavioral equivalence is mediated by a representation of a leopard per se or of the response to be made to it is difficult to resolve without experiments like that of Evans and Evans (2007) in which presentation of food was used to directly manipulate chickens' food representations, experiments that may be impossible to do with this system (but see Zuberbühler 2000a).

14.2.5 Ground squirrels and meerkats: Meaning or emotion?

Some species of ground squirrels have different calls and behaviors for snakes and aerial predators, but these are better predicted by the immediacy of threat posed by the predator than by what kind of predator it is (Macedonia and Evans 1993; Blumstein 2007). An aerial predator at a distance is responded to in the same way as a carnivore like a fox or dog, whereas a carnivore close by elicits the calls usually given to an aerial predator. The imminence of predatory threat is reflected in other ground squirrels' responses to the calls, for example in whether they run into their burrows or just stand alert. It is not necessary to interpret such calls as conveying information about the world. Rather they express the caller's emotion, something like "afraid" or "very afraid," and these emotional expressions evoke responses in listeners just as the male stickleback's "expression" of sexual readiness evokes approach in a female stickleback.

The fact that some animal communication is primarily emotional has led to claims that analyses in terms of information are unnecessary and uncalled for (Owren and Rendall 2001). But there are several reasons to see this claim as too extreme (Seyfarth and Cheney 2003b). *(1)* Some systems such as the ground squirrels' alarm calling may primarily involve emotional intensity, but that need not mean all do. *(2)* Emotion and information are not mutually exclusive. A signal that expresses the sender's emotion can still convey information to receivers. In an example suggested by Premack (see Seyfarth and Cheney 2003b), a person might make a certain delighted exclamation when and only when she finds strawberries. This exclamation both expresses the sender's emotion and tells receivers that strawberries are present. *(3)* In principle, signals can be both motivational (or emotional) and referential at the same time. An example of such a system is the alarm calling of meerkats (or suricates, *Suricata suricatta*).

Like the vervets, meerkats live in groups in fairly open terrain (here, the South African semidesert) where they are threatened by snakes, aerial predators, and ground predators such as jackals. Like the vervets too, they have acoustically distinct alarm calls and distinct responses for these three classes of predator, but in addition nearby predators elicit louder, longer, and noisier calls than those farther away. Analysis of the structure of calls given to the three predator types at different distances showed that they cluster according to both predator and distance, or threat level (Figure 14.14; Manser 2001). When recordings from the different categories were played to groups of foraging meerkats, their responses varied appropriately (Manser, Bell, and Fletcher 2001). For instance, in response to aerial alarms they scanned the sky and perhaps ran into the nearest bolthole, whereas in response to snake alarms they gathered together and approached the speaker as if preparing to mob a snake. High-urgency alarms elicited more complete and long-lasting responses than low-urgency alarms, after which the animals might only pause briefly while digging in the sand for invertebrates.

A particularly clear example of how quantitative variation in a single call type elicits parallel variations in a single type of response by listeners comes from alarm calling by black-capped chickadees (Templeton, Greene, and Davis 2005). When chickadees sight a perched owl or hawk or a small mammalian predator such as a cat, they emit "chickadee" alarm calls and gather together to mob the predator. The number of "dee" notes in the calls turns out to vary inversely with the size of predator (Figure 14.15), reflecting the fact that small maneuverable raptors such as kestrels actually pose a greater risk to small birds than do large species such as great horned

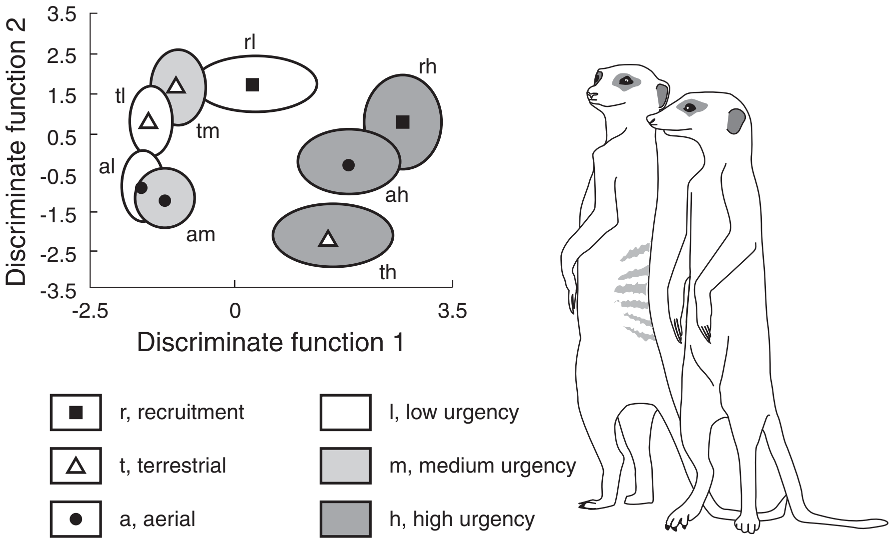


Figure 14.14. Two-dimensional discriminant analysis of meerkat alarm calls showing how they cluster by what is signaled: (terrestrial predator, aerial predator, recruitment (for example, to mob a snake), and by urgency or nearness of the threat to the group. For explanation of how such plots are constructed see Figures 6.4 and 6.5. After Manser (2001) with permission.

owls. Accordingly, playbacks of calls given to small predators evoke more calling and more approaches to the speaker than calls given to large predators. Thus the calls pass the test of functional reference, but they convey only information about risk or emotional intensity. Because they do contain information, other small birds that flock with chickadees learn their significance and join in mobbing the predator (Templeton and Greene 2007).

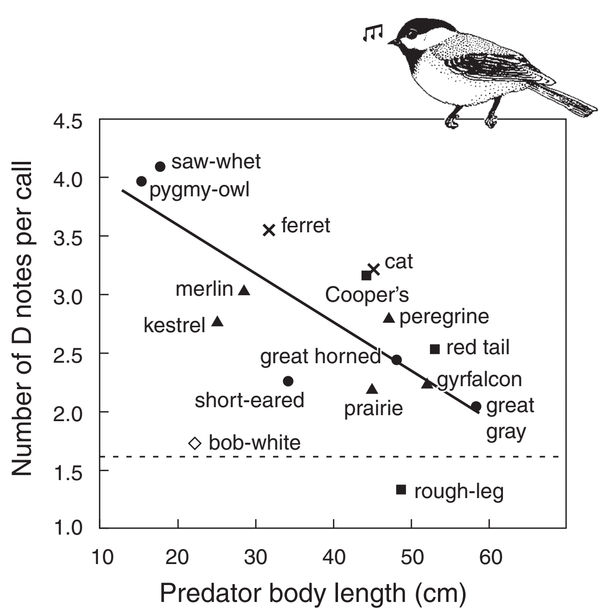


Figure 14.15. Number of "dee" notes in black-capped chickadee alarm calls varies inversely with size of predator, reflecting the fact that smaller owls and hawks are more dangerous to chickadees. After Templeton, Greene, and Davis (2005) with permission.

14.2.6 The evolution of functional reference

Comparing the systems for alarm calling and responding to alarm calls described in the last few sections suggests that the specificity of alarms reflects the specificity of evasive techniques available for different kinds of predators (Macedonia and Evans 1993; Donaldson, Lachmann, and Bergstrom 2007; Manser 2009). For instance, ground squirrels' only escape from predators in open grasslands is underground in their burrows, whereas diana monkeys in the rainforest can either descend from the canopy or climb higher. As a further example, chickens' aerial alarm calls are fairly indiscriminate (Figure 14.11), but since birds generally have very good vision this is unlikely to mean that chickens cannot discriminate among things in the air. Indeed, three species of lapwings make finer discriminations among predators than do chickens (Walters 1990). For instance, Southern lapwings have three different antipredator responses. These include swooping and pecking at snakes and displaying with wings raised at cattle approaching a nest, presumably with the function of scaring off these predators. The birds' responses to raptors and other large birds depends on the species of predator, on whether the threatening bird is perching or flying, and on whether the lapwing itself has eggs or young in the nest. Walters (1990) suggests that the difference in specificity of antipredator behavior between chickens and lapwings can be related to differences in their habitat and concomitant differences in the relative costs and benefits of correctly detecting predators versus making false alarms. Wild junglefowl, the species ancestral to domestic chickens, live—as their name suggests—in the jungle, where predators are likely to be well concealed until they are nearby. Here it might be important to have a low threshold for alarm calling because any sign of a predator likely means attack is imminent. Making fine discriminations may not be worth the risk in possible decision time lost. In contrast, lapwings live in open habitat where predators can be sighted from afar. If they reacted to anything remotely like a predator they might not have much time left for anything else, and because they can detect distant threats, they have plenty of time to take evasive action.

Comparisons among primates reveal the same relationship between habitat and predator discrimination. For example, Macedonia (1990) compared the antipredator responses of two species of lemurs living in large enclosures. Ring-tailed lemurs (*Lemur catta*), which normally inhabit areas much like those inhabited by vervet monkeys, have different calls and different evasive behaviors for ground versus aerial predators. Each call and type of behavior is characteristic of the type of threat, not its intensity. For instance, calls stimulated by a stuffed owl perched in the lemurs' enclosure or by a hawk silhouette pulled over the enclosure on wires were all aerial alarms, even though the "flying" hawk presumably represented a more immediate danger (Pereira and Macedonia 1991). Ruffed lemurs (*Varecia variegata variegata*) are larger than ringtailed lemurs or vervet monkeys and spend much of their time in dense tree canopy. Although they have more than one alarm call, the responses to these calls are not well differentiated and some of them are given in situations of high arousal not involving predators. Thus their calls do not seem to be functionally referential (Macedonia 1990; Macedonia and Evans 1993). As with ground squirrels, in the ruffed lemurs' habitat imminence may be the only feature of predators that matters. However a comparison of sympatric cape ground squirrels and meerkats (Furrer and Manser 2009) shows that social structure and how a species uses its habitat may also play a role.

All these observations suggest that in evolution as in some category learning experiments, animals come to group multiple stimuli by required response, not necessarily by perceptual similarity. A recent model of the evolution of signaling systems (Donaldson, Lachmann, and Bergstrom 2007) demonstrates exactly this: functional reference evolves when the world is structured so that different classes of situations require different responses. Risk- or intensity-based systems evolve when all that is available is variation in one type of response. Many social species have food calls as well as alarm calls; we have seen an example in fowl. Receivers clearly need to discriminate food calls from alarm calls, but about all food calls have been shown to do is to attract other animals (e.g., Hauser 1998; Pollick, Gouzoules, and De Waal 2005). Thus food calls and alarm calls meet the criteria for functional reference in that the one evokes approach and the other species-specific defensive behaviors, but such a simple system communicates only motivation. A further important factor in signal evolution is social structure (see Hauser 1996; Blumstein 2007). Signaling should evolve as a function of the degree to which the signal can influence kin or long-term companions that may reciprocate in future. Since signaling may be costly if it attracts a predator's attention, we should expect alarm calling to evolve only when single individuals are likely to spot a source of danger before their companions and be in a position to warn relatives or possible reciprocal altruists (Chapter 12).

14.3 Trying to teach human language to other species

Attempts to teach human language to chimpanzees and other animals have a long history (see Candland 1993). To some extent, they are the expression of an enduring human wish to communicate with other species (Candland 1993) or, as the title of one book (Bright 1990) puts it, "The Dolittle Obsession." The last half of the twentieth century saw a series of much-publicized and controversial attempts to teach various forms of human language to chimpanzees and other great apes. Although the accomplishments of these animals seem impressive, there is much about them to debate. The various animal language projects have been extensively reviewed by both proponents and critics (e.g., Wallman 1992; Rumbaugh and Savage-Rumbaugh 1994; Ristau 1996). It is now generally accepted that the earliest projects did not succeed in doing much more than teach chimpanzees a lot of clever tricks. Later projects may or may not have overcome all of the problems of the earlier ones. One animal, Kanzi the bonobo, is reported to have reached a level of comprehension of spoken English comparable to that of a two-year-old child. Arguably, however, taken all together the results of "animal language" studies are most revealing for what the animals did *not* do (Fitch 2005). In any case, the first question that needs to be addressed is what would it mean if members of another species either did or did not acquire a form of human language?

14.3.1 What can we learn?

"Can any animals learn language?"

To begin with, "Can animals learn language?" is the wrong question. As we have seen, several features of language are shared by the natural communication systems of some other species. The candidates for features uniquely characteristic of human language include semanticity, productivity, duality, and recursion (see also Pinker and Jackendoff 2005). The first two are linked in attempts to see whether the animals combine the signs they learn in orderly ways to create new meanings because doing so could imply an understanding of simple linguistic structure. Some of the research with apes has used a system that potentially has duality, that is, in principle the language user could both comprehend and produce the words and sentences of the language. This makes it possible to ask whether subjects actually understand all that they can produce and to probe knowledge of syntax with tests of comprehension. However, syntax is more than discriminative responding to word order. It entails knowledge of the interrelationships among structures in the language. For instance, the native speaker of English knows not only that “Tim gave the apple to Lana” means something different from “Lana gave the apple to Tim.” She also knows the relationship of these statements to other grammatical sentences such as “To whom did Tim give the apple?” and “Was the apple given by Tim to Lana?”

Attempts to teach forms of human language to apes were bedeviled by the problem of formulating clear behavioral criteria for language in part because while the research was going on so was research and theorizing about human language. Among other developments were advances in understanding language acquisition in children and language use in deaf users of American Sign Language, which was taught to some of the apes. Closer looks at what actually goes on as children acquire their first words and sentences were stimulated to some extent by the ape language research (Seidenberg and Petitto 1987). Some of these developments made the chimpanzee subjects of language training experiments look less like humans than they first appeared.

“Are apes like young children?”

Even if animals cannot be taught to converse like human adults, some have thought they might at least have a childlike grasp of language. Thus, apes exposed to forms of human language might reasonably be compared to young children in their achievements and how they reach them. The results of such comparisons have much in common with those from the comparisons of swamp sparrows and song sparrows mentioned in Chapter 1 (Figure 1.3): when members of two species are exposed to experiences characteristic of the species-typical development of one of them, they are influenced in very different ways. Each species of sparrow learns only its own song, and similarly, when child and chimpanzee are exposed to the child’s species-typical experiences, even if some of those experiences affect both similarly, ultimately the chimpanzee does not develop in the same way as the child.

“Does language acquisition reflect a general learning ability or a specialized module?”

All hearing children except those suffering extreme social deprivation acquire the spoken language used by those around them, and they do so with very little direct teaching. Even deaf children learning to sign develop language in a predictable way across cultures (Pinker 1994). Still, just as in other species, adults have some special ways of behaving around their young that provide conditions conducive to learning. Mothers talk to their babies and toddlers in very simplified, repetitive, language, “motherese.” Language development also depends on specifically social cognitive modules, in particular shared attention (cf. Chapter 12; Tomasello et al. 2005). A child knows what an adult is talking about because she knows what the adult is attending to. The similarity of all human languages in abstract structure together with the similarity in the way they are acquired led Chomsky (1968) to the idea of a species-specific Universal Grammar. This is the output of a species-specific Language Acquisition Device, or language module. This nativist view of language was opposed in the 1960s by Skinner's explanation of language as just another operant behavior, a view that is now largely discounted. The fact that language-trained apes, dolphins, or parrots do not learn more than rudimentary elements of linguistic behavior, at best, is one reason why it should be. Nevertheless, any evidence that a component of linguistic competence is acquired by a nonhuman animal, especially one not closely related to humans (see Box 14.1) indicates that at least that component of language can be generated by some sort of general learning ability.

"How did human language evolve?"

The Chomskian view implies that language represents a major discontinuity in evolution. The issue of how something so complex, abstract, and specialized might have evolved is controversial and much discussed by brain anatomists, anthropologists, and human behavioral ecologists, among others (Christiansen and Kirby 2003; Maynard Smith and Harper 2003; Fitch 2005; Fitch, Hauser, and Chomsky 2005; Pinker and Jackendoff 2005). In the present context the issue is simply what, if anything, the effects of exposing apes or other species to language training can tell us about language evolution. A point often made (e.g., Rumbaugh and Savage-Rumbaugh 1994) in support of ape language projects is that the results must be

Box 14.1 Fast Mapping by a Dog?

When 2- to 3-year-old children are learning language their vocabulary increases at an amazing rate, in part through a process of rapid word learning known in linguistics as *fast mapping*. Fast mapping is demonstrated experimentally when a toddler is shown a novel object or action labeled with a new word: "This (funny object) is a *dax*." Or the toddler might be shown the novel object along with familiar ones and asked to indicate the *dax*. Importantly, from such minimal experience the young child does not simply form a new sound-object association, but implicitly understands the sound as a *word,* that is, a sound with referential and grammatical properties. For instance, she can use and understand it in new sentences ("Where is the dax now?" "This dax is green.") Fast mapping has been claimed as one specialized component of human linguistic ability (Bloom 2004), but at least one animal, a highly trained border collie named Rico, learns in a way that is superficially similar (Kaminski, Call, and Fischer 2004).

At the time he was tested Rico knew the names of about 200 objects in that he would correctly retrieve them when told to. The demonstration of fast mapping consisted of Rico's owner telling Rico to go into an adjacent room and fetch something from a collection of 8 items, one of which was novel. On 70% of trials when a novel word was used, he fetched the novel item. Retention was tested similarly four weeks later, but now Rico had to choose the target, presumably learned, item from a collection of four completely novel and two or three familiar items. He was correct on three out of six such tests (chance was about 1/8) and chose one of the novel items when he was incorrect.

On one view (Kaminski, Call, and Fischer 2004), Rico's performance demonstrates that one of the building blocks of language is present in other species, at least under conditions of extensive prior experience with words as labels. However, on another (Bloom 2004; Markman and Abelev 2004). Rico's undeniably impressive ability is not the same as learning words. A potential methodological problem is the lack of controls for novelty preference which are usually used with children (Markman and Abelev 2004). Would Rico choose the novel object in a set if simply asked to "fetch"? More importantly, as illustrated in Figure B14.1, does Rico understand the labels he knows referentially or simply as part of a command ("fetch-the-sock")? Can he, for example, learn new words in other ways, as by being shown the object being named, and transfer this knowledge to other contexts (Bloom 2004)?

Whatever the results of further studies with Rico or similarly trained animals, it is worth noting that learning the significance of a novel stimulus in the way he apparently did, namely, by excluding familiar ones, is not unique to this study. A nice example comes from two sea lions trained on matching to sample with two 10-member equivalence classes, essentially numbers and letters (Kastak and Schusterman 2002). For instance, when one of the "numbers" was the sample, the sea lion had to match it with any one one in the "number" class, avoiding an alternative in the "letter" class. Learning by exclusion was demonstrated by following a familiar number sample with a novel symbol and a known letter. The sea lions chose the novel symbol above chance and learned it as a number, whereas if the sample was a letter in this example, a familiar letter comparison would be chosen and the novel symbol avoided. In either kind of case, symbols first encountered in this way then served as samples in normal trials with familiar letters and numbers as comparisons. One animal correctly matched them immediately, and the other with very little experience.

Inference by exclusion is a related ability. In an early example (Premack and Premack 1994) chimpanzees watched as two containers were baited, one with banana and one with apple. With the containers hidden behind a screen, an experimenter removed one of the fruits and ate it in view of the subject. Inferring that the container with that item is empty should lead to choosing the other container. As a group four chimpanzees performed at chance on the first test, although some learning occurred when the test was repeated. A larger group of great apes tested similarly performed above chance on their first trial (Call 2006), but not as well as the four-year-old children tested by Premack and Premack (1994), 90% of whom chose correctly the first time. Other species have also been tested on various paradigms designed to tap inference by exclusion (see Aust et al. 2008) but with little evidence of immediate successful performance.

Figure B14.1. Cartoon depiction of two ways in which Rico could understand names of things in commands such as "fetch the sock": as a word referring to an object (left) or as part of a command for a particular action. After Bloom (2004) with permission.

relevant to human language evolution because the great apes are our closest living relatives (see Hauser 2005). One problem with this line of reasoning is that “closest living relative” has no special status (Pinker 1994). If all extant nonhuman primates went extinct tomorrow, some other mammal would be our closest living relative, but that would not mean that studying it would shed any special light on language evolution. Yet-untold numbers of hominid species have come and gone since the last common ancestor of apes and humans. Because language may have appeared first in a hominid species that is now extinct, at most apes’ linguistic abilities can tell us what was present in the most recent common ancestor of apes and humans. They are silent on when, why, and how full human language subsequently evolved. Arguably we will learn more about language evolution by studying other animals’ natural communicative and conceptual abilities (Section 14.4).

14.3.2 Washoe, Nim, Sarah, and Lana

The immediate precursors of more contemporary ape language projects were two projects in the 1930s and 1940s in which husband-and-wife psychologists—the Kelloggs and later the Hayeses—raised a young chimpanzee like a child for periods of a few months to several years. Both of these animals, Gua and Viki, could communicate and solve problems, sometimes better than children of the same age, and Viki was eventually shaped to make vocalizations that could be understood as “mama,” “papa” and “cup.” Overall, however, the results led to the conclusion that chimpanzees could not actually talk, probably because they lacked the neural and anatomical requisites for speech. But clearly this does not mean that they might not be able to communicate linguistically using a medium more within their grasp, and that insight inspired a series of subsequent projects.

In the first of these, Beatrice and Allen Gardner attempted to teach American Sign Language (ASL) to the infant chimpanzee Washoe (Gardner and Gardner 1969). As much research has revealed since the Gardners’ work began, ASL is a sophisticated natural language that is acquired and used like spoken language (see Pinker 1994; Ristau 1996). Washoe was surrounded by people who signed but did not speak in the hopes that she would acquire signing spontaneously as deaf children do. Shaping and explicit instrumental reinforcement were also used. After 22 months, Washoe was judged to know 30 signs, and eventually she was reported to use over 100. Much of the data collection on which these numbers were based went on during the course of daily free behavior—going for walks, eating, looking at magazines, playing. Use of signs was recorded from memory after the event. Later Washoe was given structured vocabulary tests in which she signed the names of objects that could not be seen by the person interpreting the signs. Later too, more emphasis was given to the question of whether combinations of signs constituted sentences. Particularly interesting was the possibility that Washoe combined her signs in novel but meaningful ways. For instance, she was reported to sign “water bird” for a swan. The ways in which this report might suffer from all the usual problems with anecdotes need hardly be mentioned.

The Gardners’ 1969 *Science* paper marked the beginning of an optimistic outpouring of projects with nonvocal languages. The optimism lasted until 1979, and the publication, also in *Science,* of a deflationary article by Terrace, Petitto, Sanders, and Bever entitled “Can an ape create a sentence?” (Terrace et al. 1979). These authors had trained an infant chimpanzee, Nim, in ASL using similar methods to the Gardners. Like Washoe, Nim learned to make many different signs and eventually produced them in combinations of two, three, or more (Figure 14.16). His two-sign

Figure 14.16. Nim signing "me" and "hug." From photographs in Terrace et al. (1979) with permission.

combinations did have structure. For instance many combinations consisted of *me* or *Nim* as agent or object of an action, as in "me drink" or "hug Nim." However, when it came to longer utterances, the resemblance to child language vanished. As a young child matures and acquires a larger vocabulary, the mean number of words per utterance increases dramatically. The same was not true of Nim. Even though his vocabulary increased to 125 signs by the end of the 4-year project, the mean length of his "utterances" stayed about the same (Figure 14.17). More important, when he did combine three or more signs, the added signs usually repeated those already given, as in "play me Nim play" or "grape eat Nim eat."

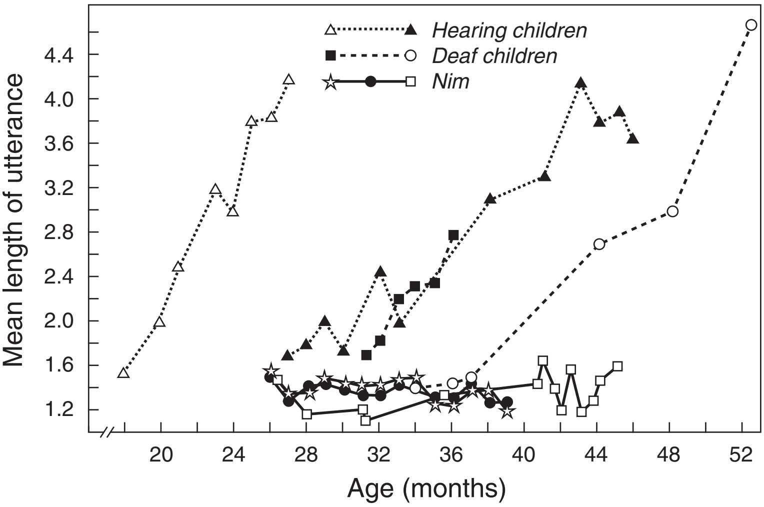


Figure 14.17. Changes in mean length of Nim's utterances over time compared to data from two hearing and two deaf children. Nim's data were recorded in three kinds of circumstances, represented by the three symbols. Redrawn from Terrace et al. (1979) with permission.

Terrace et al.'s most devastating conclusion came from an analysis of filmed interactions between Nim and his trainers. These revealed that very often Nim's signs were simple repetitions of signs that had just been made by the trainer. This same effect was evident in commercially available films of Washoe that Terrace et al. analyzed, much to the consternation of the Gardners (see Ristau and Robbins 1982). The tendency simply to imitate what was just signed is but one of several ways in which the chimpanzee's use of signs is unlike the child's use of language. Children engage in conversation, which means taking turns to exchange information. Children also use language to talk about the world, apparently for sheer pleasure in naming and commenting on things (see Pinker 1994). In contrast, the signing apes tended to "talk out of turn" (Terrace et al. 1979) and seldom used signs other than as instrumental responses. In short, Terrace et al. concluded that the answer to the question posed in the title of their article was a resounding "No." A more recent analysis of extensive filmed records of signing by Washoe and four other chimpanzees trained in the Gardners' program (Rivas 2005) gave results entirely consistent with Terrace et al.'s.

Two other chimpanzee language training projects started in the late 1960s used invented nonvocal languages of visual symbols. The chimpanzee Sarah was trained by Premack (e.g., 1971) to use a system of plastic shapes, and Lana was the first of a continuing series of apes trained by Rumbaugh, Savage-Rumbaugh and associates to use "Yerkish" symbols on computer keys (e.g., Rumbaugh 1977; Savage-Rumbaugh 1986). When the animal communicates by touching plastic shapes or computer keys, it is no longer necessary to rely on trainers who sign, in some cases inexpertly and in nonstandardized ways. There is less ambiguity in the animal's "words" since there is less chance of overinterpreting the choice of a symbol than a movement of the animal's hands. With the computer system it is also possible in principle to record and analyze the subject's entire linguistic input and output (for a thoughtful analysis see Ristau and Robbins 1982; Ristau 1996). On the other hand, confining the animal's linguistic experience to sessions in front of a keyboard limits the possibility for spontaneous communication and makes more apparent the parallels between this form of "language training" and straightforward operant conditioning.

The chimpanzee Sarah was trained with standard operant conditioning methods to associate plastic tokens of various colors and shapes with the objects they "named," in effect learning symbolic matching to sample (Premack 1971). Once Sarah had acquired some vocabulary, the project focused on using the token system to probe her grasp of concepts like *same/different, color of, name of* (Figure 14.18). Rather than a study of chimpanzee language learning it became a test of more general conceptual and problem-solving abilities, such as analogical reasoning (see Premack and Premack 1983). It was claimed that language training had fostered Sarah's apparent abstract reasoning abilities.

In the artificial communication system used first with Lana chimpanzee, the "words" are geometric designs on plastic keys connected to a computer (Figure 14.19; Rumbaugh 1977). Like the animals in other early projects, Lana interacted with the symbol system primarily to get things she wanted. The computer was programmed to activate appropriate dispensers upon receipt of grammatical strings like "Please machine give apple" and "Please machine give drink." Not surprisingly, what Lana learned mirrored the contingencies built into this system. Her behavior could be accounted for as associations between actions, people, or objects and symbols that could be plugged into six stock sentences such as "please (person) (action)" (C. Thompson and Church 1980). Even those who promoted the

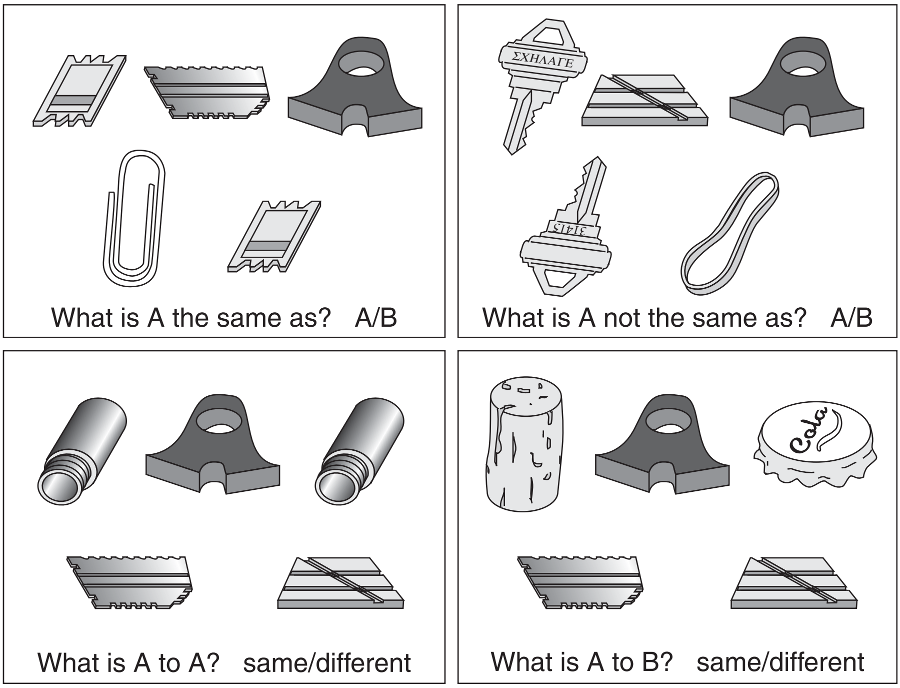


Figure 14.18. Questions about same/different relationships as represented in the system of tokens used to train Sarah the chimpanzee. In the two problems in the top row, Sarah had to choose the correct (matching or nonmatching) object. In the lower pair of questions she had to choose the token corresponding to "same" or "different." From Premack and Premack (1983) with permission.

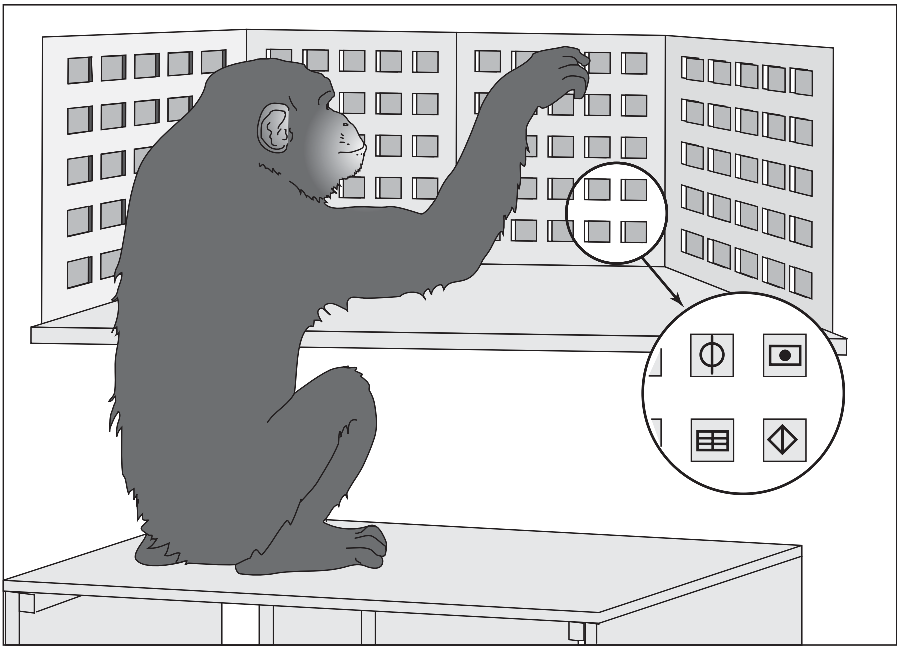


Figure 14.19. Lana working at her keyboard. From the frontispiece of Rumbaugh (1977) with permission.

Lana project at the time eventually agreed that any training regime in which "words" are used primarily as operants to obtain food and activities does not promote genuine linguistic competence, even if chimpanzees might be capable of it (e.g., Rumbaugh, Savage-Rumbaugh, and Sevcik 1994).

14.3.3 Sherman and Austin, Jack and Jill

Lana was replaced as a student of Yerkish by Sherman and Austin, but work with them emphasized the interrelationships of production and comprehension, the social use of language, and what the symbols meant to the animals. Syntax was less emphasized, perhaps correctly, given the difficulty of distinguishing rudimentary syntax from sequence learning. Sherman and Austin were taught to name foods and other things by being rewarded with something other than the object being named. For instance, Sherman might be shown a banana and asked (in Yerkish symbols, *lexigrams)* "What this?" If he selected the lexigram for *banana* in reply, he received praise or the opportunity to request a different food, but not a piece of banana (Savage-Rumbaugh 1986). Notice that formally this skill is like symbolic matching to sample or category learning: the animal is exposed to a sample, selects a response, and is reinforced. To continue this analogy, Sherman and Austin were also trained in a form of delayed matching to sample, in which they were shown a food or other interesting object in one room and then led back to their keyboard in a different room and asked to describe or request what they had seen. At a later stage, they were encouraged to use lexigrams to specify what they were about to do or wanted to do (Savage-Rumbaugh et al. 1983; Savage-Rumbaugh 1986). For instance, to see if an animal "knew what he was saying" when requesting a tool, he might be presented with the whole tool kit to see if he chose the tool he had asked for, which Sherman and Austin did at better than chance levels. Naming and requesting were combined with other skills in a situation described as "Symbolic communication between two chimpanzees" (Savage-Rumbaugh, Rumbaugh, and Boysen 1978). Sherman and Austin were induced to request and share food with one another through the mediation of lexigrams. Now one animal "informed" the other of the contents of a food container, the second animal requested some of the contents, and if both were correct, they both got some of it to eat. There are parallels here with the attempts to establish the functional reference of natural signals (Section 14.2), in that the animals have to both produce and respond to the signal appropriately.

As the preceding summary implies, many of the elements of Sherman and Austin's behavior can be described as instrumental discriminations. This was underlined by a tongue-in-cheek report of a simulation of Sherman and Austin's performance by two pigeons, Jack and Jill (Epstein, Lanza, and Skinner 1980). With conventional procedures of shaping and selective reinforcement, Jack was trained to ask Jill the color of a light hidden under a curtain by pecking a "what color?" key, and Jill was trained to report it to Jack by pecking a color name. Jack evidenced his understanding of Jill's report by pecking the selected color and then a "Thank you" key (Figure 14.20). When both birds performed correctly, both were reinforced with grain. Borrowing the words of Savage-Rumbaugh, Rumbaugh, and Boysen (1978), Epstein et al. concluded, "We have thus demonstrated that pigeons can learn to engage in a sustained and natural conversation without human intervention, and that one pigeon can transmit information to another entirely through the use of symbols" (Epstein, Lanza, and Skinner 1980, 545). Whether this demonstration captures everything about the processes underlying the chimpanzees' behavior is of course debatable.

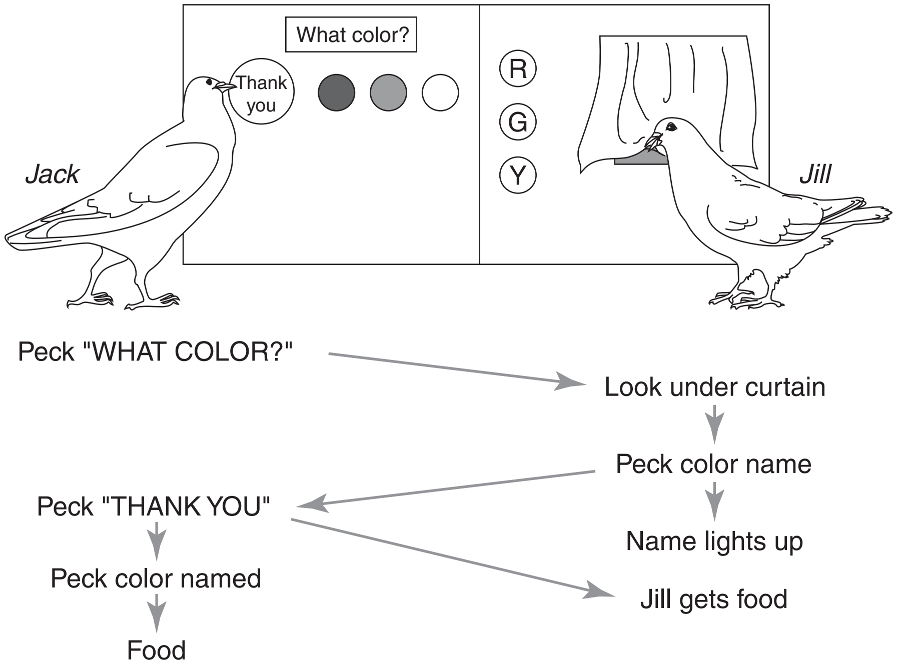


Figure 14.20. Setup and procedure for the demonstration of "communication between two pigeons." After Epstein, Lanza, and Skinner (1980) with permission.

14.3.4 Kanzi the bonobo

Bonobos are so-called pygmy chimpanzees (*Pan paniscus*); previous chimpanzee subjects of language-training projects had all been common chimpanzees (*Pan troglogytes*). Kanzi the bonobo has two accomplishments that set him apart from previously trained apes. First, he learned to use and understand lexigrams through observing his foster mother being taught them (Savage-Rumbaugh et al. 1986). Second, he understands human speech. When Savage-Rumbaugh and her colleagues realized Kanzi had evidently acquired his Yerkish and English comprehension skills simply through observation, much as young children initially comprehend much more than they can produce, they turned to investigating how far he could go if treated more like a young child. He was allowed to roam through a 55-acre wooded area where he could find food and all sorts of experiences, always accompanied by people talking while communicating on portable keyboards about what was happening or about to happen.

Kanzi's understanding of spoken English sentences was directly compared to that of a 2-year-old child in a controlled way (Savage-Rumbaugh et al. 1993). Both Kanzi and Alia, the child, were asked to carry out instructions expressed by simple sentences like "Get the telephone that's outdoors" or "Make the doggie bite the snake." A variety of objects was present, and the two subjects were asked to do several actions with each one rather than just the obvious ones. Importantly, these tests employed some completely novel sentences (see Savage-Rumbaugh and Brakke 1996). Precautions were taken against cuing by the person giving the instructions and selective recording by the raters. For instance, in some tests the other people recording data wore headphones broadcasting loud music so they would not know what Kanzi had been asked to do. Kanzi performed comparably to Alia on these tests. In other tests, his competence at producing sentences with lexigrams was comparable to that of a 1.5-year-old. These results can be taken to indicate that Kanzi learned more than to perform complex operants to get what he wanted but rather could use and understand words and sequences of words as representations of states of the world (Savage-Rumbaugh et al. 1993; Rumbaugh and Savage-Rumbaugh 1994 but see Seidenberg and Petitto 1987).

Does Kanzi's performance represent a species difference between bonobos and chimpanzees? Given the threat to both species in the wild, not to mention the expense and labor involved in raising them with a rich experience of spoken and symbolic language, it is unlikely that the data required to answer this question will ever be collected. However, a few bonobos have been studied, and it does appear that they have a greater propensity to acquire comprehension of spoken English than chimpanzees do (Rumbaugh and Savage-Rumbaugh 1994). So far it is not at all clear why they would be expected to be especially likely to learn human language. Bonobos are not so well studied as chimpanzees in the wild, so it is not clear whether their natural communication system is more languagelike. Evolutionarily they are no more part of the hominid lineage than chimpanzees.

14.3.5 Conclusions

Besides the apes we have considered, a few orangutans and a gorilla have been exposed to various forms of language training (see Ristau 1996). Dolphins and a sea lion have been taught to obey complex systems of gestural or auditory commands (Gisiner and Schusterman 1992; Herman 2006). Although learning to obey such commands can be described as conditional discrimination learning (Schusterman and Kastak 1998), they do have some linguistic properties. Most importantly, perhaps, the sequences of commands learned by the dolphins have a simple syntax, as in "take the hoop to the ball" versus "take the ball to the hoop," and the animals are sensitive to this (Herman and Uyeyama 1999; Kako 1999). And we have already met Alex the parrot, whose ability to talk was exploited more as a way to assess what nonlinguistic concepts he could acquire or express than for its possible relevance to language learning (Pepperberg 1999). He too demonstrated sensitivity to some properties of language, for example once learning a new word in one context (e.g., "rose" as the color of a paper) he transferred it to a new one ("rose wood") and responded correctly to it in new kinds of sentences (Kako 1999). Such findings lend support to proposals that at least some components of human language reflect cognitive competencies shared with other species (Herman and Uyeyama 1999).

Animal language-training projects raise many issues that are common to other areas of comparative cognition. These include the need for unambiguous behavioral criteria when testing another species for an essentially human cognitive process, the problems of Clever Hans and overinterpreted results, the shortcomings of anecdotes and single-subject studies, and the relative roles of general processes of learning versus modularity and species-specificity. The novel issues have to do with what constitutes human language and how it develops in very young children. Much of the controversy here boils down to disagreement over whether or not the subjects are "merely" demonstrating instrumental responding. Paradoxically, even though experience of conditioning procedures is increasingly shown to lead to complex and subtle representations of the world (Chapters 4, 6, 11), interpreting animals' communicative behaviors as resulting from associative learning is taken to rob them of interesting cognitive content. Consider, for example, the experiments of Holland and others reviewed in Chapter 4 in which rats behave as if a Pavlovian CS evokes an image of its associated US, an image that can itself support new learning. Don't these findings mean the CS has acquired a simple kind of meaning for the rat?

Another anomaly is that any demonstration that linguistic output, whether it be vocalizing, pressing symbols, or responding to spoken commands, can be explained as simple discrimination learning is taken as showing that the subjects are not doing what a young child would do in similar circumstances. Yet simple associative learning may well explain some of the young child's early responses to speech, and some of the child's early sentences may be no more complex than Lana's stock sentences (Seidenberg and Petitto 1987). One may note that Kanzi acquired his comprehension of spoken English only after intensive exposure and an extraordinary amount of attention from human companions, but such experience is the norm for young children. If language exposure and "enculturation" through extensive interactions with humans changes apes' cognition as some have claimed (e.g., Premack 1983; Savage-Rumbaugh and Brakke 1996; Tomasello and Call 1997), then maybe some of the same changes are involved in aspects of child language acquisition. Yet the difference remains that the child's early language rapidly develops into an elaborate and unique form of communication that no other primate ever shows. This profound species differences has generated a whole range of experimentation, theorizing, and debate, some of which is sketched in the next section.

14.4 Language evolution and animal communication: New directions

Theorizing about the evolution of human language is a vast and active area in itself, nowadays one that integrates genetics, cognitive neuroscience, and mathematical modeling with more traditional studies of the nature and development of language (Christiansen and Kirby 2003; Fitch 2005; Fisher and Marcus 2006). Most relevant in the context of this book is how information about the communication systems of other species can contribute to this enterprise. The analysis of apparent "fast mapping" in a dog, summarized in Box 14.1, is an example. The neural and behavioral parallels between birds' song learning and humans' language acquisition (Box 13.2) apparently reveal general constraints on learning and producing complex sounds. And unlike in these examples, discovery that any components of language are shared only with apes or only with nonhuman primates would be indicative of some genetic, neural, and/or other factors specific to our own lineage. Not surprisingly then, the wealth of recent information about communication in other species is increasingly being brought to bear on discussions about the nature and evolution of language (Fitch 2005; Jackendoff and Pinker 2005; Weiss and Newport 2006; Hauser, Barner, and O'Donnell 2007).

One focus of these discussions has been the distinction proposed by Hauser, Chomsky, and Fitch (2002) between the human language faculty in the broad sense (*FLB*) and the faculty of language in the narrow sense (*FLN*). FLB includes all the perceptual, motor, and cognitive abilities that contribute to language but are shared with other species and/or used in other domains, whereas FLN includes only those components essential to language and unique to humans. Hauser, Chomsky, and Fitch further proposed that FLN consists solely of recursion, that is, the ability to understand and produce recursive structures. This is essentially an extension of Chomsky's (e.g., 1968) original, seminal, proposal that the essentials of language are in its underlying structure rather than in superficial features like how it is produced. The proposed distinction between FLB and FLN is controversial. A prominent alternative view (Fitch, Hauser, and Chomsky 2005; Pinker and Jackendoff 2005) is that indeed many components of human linguistic ability are shared with other species, but in the evolution of human language they have become uniquely coadapted for communication, that is, no one particular skill corresponds to FLN.

Although even human babies can discriminate recursive auditory structures, Hauser and colleagues' proposal implies that no nonhumans can. This implication has been tested by asking whether animals can discriminate strings of sounds that obey a phrase *structure grammar* from those that obey a simpler *finite state grammar* (Figure 14.21). Recognizing a string that obeys a grammar of the first type requires tracking dependencies across several elements, as in "John, while he was dancing a jig, was singing." Finite state grammar, in contrast, entails only stringing grammatical units together, as in "John was dancing a jig, and he was singing." Formally, the first is an *AABB* string, and the second, *ABAB* (Here the subject, John, is *A,* and *B* is the verb.). Tamarins and Harvard students were exposed to strings of nonsense syllables, the "A" syllables spoken by a female and "B's" by a male (Fitch and Hauser 2004). *A* and *B* were each represented by eight different sounds, with a different pair used in each instance of the string. One subgroup from each species heard strings described by a grammar of each type. The students pressed a key to indicate whether new strings had the same pattern as those they had heard. A habituation/dishabituation paradigm was used for the tamarins. After they were familiarized with their training strings, looking toward the speaker was compared for novel test strings from both grammars. Importantly, the same test stimuli were presented to tamarins from both groups. Those trained with the finite state grammar discriminated ABAB . . . strings from AA . . . BB strings, looking longer toward the speaker for strings with the unfamiliar structure, but those trained with

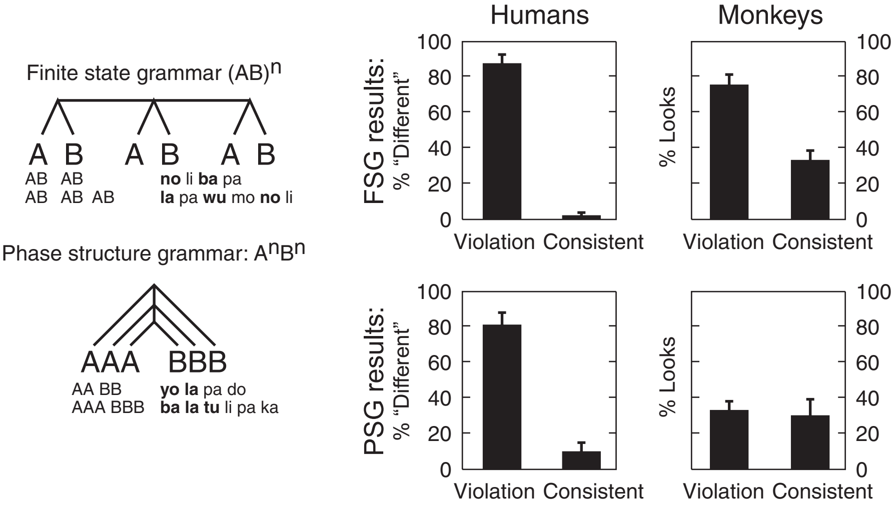


Figure 14.21. Diagrams on left show examples of finite state (nonrecursive) and phrase structure grammars (FSG and PSG) as used by Fitch and Hauser (2004) to test humans and tamarins. Histograms compare the species' ability to detect a difference between the two types of strings as a function of the type they were trained on. Adapted with permission.

the phrase structure grammar did not. As shown in Figure 14.21, the monkeys in this group looked rather little under both conditions, as if they had encoded the training stimuli as unstructured strings of sounds, which were by now rather uninteresting. The students, in contrast, discriminated almost perfectly regardless of training condition.

One problem with a claim that *no* species other than humans can do something is that it is impossible to prove. At the same time, such a claim raises the irresistible and possibly infinite challenge of finding a species and a circumstance in which whatever it is can be demonstrated. When it comes to testing sensitivity to the structure of sound sequences, songbirds would seem to be obvious subjects, and indeed, starlings trained with strings of starling syllables can learn to discriminate between the same two grammars used for the tamarins (Gentner et al. 2006). Starlings were an apt choice for this type of study because in nature they mimic the songs of many other species. However, unlike the tamarins, the starlings had thousands of trials of training with explicit reward for discriminating between the two grammars. Moreover, to succeed with AA . . . BB . . . strings the birds did not need to match corresponding A's and B's correctly as in recognizing the phrase embedded in a sentence. They needed only to detect a match between the numbers of A's and B's (Corballis 2007). That is, they may have learned a rule based on counting, not recursion. Such rule learning has even been demonstrated in rats, which learn and transfer a discrimination between sound patterns (e.g., XXY and YYX versus other sequences of the same sounds; Murphy, Mondragón, and Murphy 2008). Even if starlings pass better tests of sensitivity to recursion this would mean at most that it is independently evolved in one or more species of songbirds, that is, it is analogous not homologous to recursion in humans. Such findings would thus be consistent with the view that the uniqueness of human language is not in any one component but in how its many components are combined (Pinker and Jackendoff 2005; G. Marcus 2006).

Testing tamarins for sensitivity for recursion makes sense on the assumption that other species could possess some of the conceptual or representational components of human language without expressing them in communication. In another example (see Hauser, Barner, and O'Donnell 2007), rhesus macaques were tested to see if they spontaneously make the distinction between singular and plural sets that children make relatively early in language acquisition. Indeed, a relatively uncontroversial one of Hauser, Chomsky, and Fitch's (2002) claims is that comparative studies should be designed to look for such components of language in other species (Pinker and Jackendoff 2005; Hauser., Barner, and O'Donnell 2007). For example, even if hierarchical embedding of sound sequences eludes them, some nonhuman species may show evidence of using concepts with recursive structures in other cognitive domains. Hauser, Chomsky, and Fitch (2002) suggest spatial cognition is one such domain. A stronger candidate, in that it seems to be uniquely present in highly social primates, is hierarchical representation of social relationships (Cheney and Seyfarth 2005b). Consider, for example, the evidence that baboons classify their companions simultaneously by rank and family group (Section 6.5.5; Bergman et al. 2003). Cheney and Seyfarth (2005b) propose that in addition the information baboons acquire from others' vocalizations is referential and propositional, as in "Animal A wants to touch B's baby" or "C is threatening D." They suggest that primate social life favored the evolution of such conceptual abilities and these were eventually reflected in the structure of language, that is, in what primates expressed as well as understood. This and related discussions (e.g., Hauser, Barner, and O'Donnell 2007) have opened a new phase in the comparative study of language that draws on a broad base of laboratory and field studies of animal cognition to make inferences about the distribution of conceptual and other abilities that make human language possible.

14.5 Summary and conclusions

Many of the issues that arise in the study of communication have been considered already in this book. The contrast between ecological and anthropocentric approaches introduced in Chapter 1 is apparent in the contrast between studies of natural communication systems and attempts to teach language to other species. Other examples are how the properties of signals are matched to receivers' perceptual systems (Chapter 3) and how animals categorize stimuli (Chapter 6). Issues relevant to the behavioral ecology and evolution of signaling were touched on in the discussion of reciprocal altruism and kin recognition in Chapter 5 and elsewhere. Issues discussed in Chapter 12 reappear in discussions of whether animals send signals with the intent to modify their receivers' behavior or understanding, to deceive, or to teach, abilities which require theory of mind. So far, there is no better evidence for theory of mind here than in other realms.

In communication as elsewhere, a key issue is how to translate essentially anthropocentric concepts into predictions about observable behavior. In the context of natural communication systems, that has been done in the development of criteria for functional reference. In addition, there are important parallels between functional reference, attempts to study what "words" mean to language-trained apes, and phenomena in the study of what CSs represent in associative learning. The concepts specific to the study of communication include the terminology of *sender, receiver, message,* and *meaning*. Comparisons of animal communication to human language also entail a variety of concepts having to do with the nature of language. One of the most contentious is whether or not any animals have acquired syntax or are sensitive to recursion.

Do honey bees have language? Can apes learn human language? Attempts to answer such questions have engendered controversy in part because they seem to bear so directly on what makes us human. Darwin's (1871) claim of mental continuity between humans and other species has been severely tested when it comes to language. Macphail (1987) suggested that there are essentially no qualitative differences among vertebrates in simple associative learning and all that flows from it, such as category learning, perceptual learning, and the like. To that can be added spatial learning, timing, and numerosity discrimination. What may be unique about humans is the ability to acquire language, and this in turn may make possible self-recognition, theory of mind, consciousness. But the first part of the twenty-first century has seen an explosion of alternative proposals about human uniqueness, many of them drawing on a broad base of comparative research. We briefly evaluate some of them in the next chapter.

Further reading

The part of this chapter on natural communication systems is but a brief survey of a major area of research with vast literature of its own. The authoritative reviews remain the books by Hauser (1996) and Bradbury and Vehrenkamp (1998). The short introduction by Maynard Smith and Harper (2003) focuses on functional aspects of communication. *Animal Communication Networks* (P. McGregor 2005) covers eavesdropping and the like in species from fish to monkeys. Bird song, too, is the subject of whole books (Marler and Slabbekoorn 2004; Zeigler and Marler 2004). Catchpole and Slater is a brief and clear introduction (1995). For bees, Seeley (1995) shows how communication helps regulate a hive's resources.

Pinker's (1994) *The Language Instinct* is a prize-winning account of all aspects of language, giving plenty of attention to evolutionary and comparative issues. The chapters in *Language Evolution* (Christiansen and Kirby 2003) review much of the contemporary work. Candland (1993) provides an illuminating and often entertaining account of the long history of attempts to talk with animals and feral human children. *The Simian Tongue* (Radick 2007) is another book for the general reader, this time on the history of research on "language" in wild primates. It includes an extensive account of the field work by Marler, Cheney, and Seyfarth, whose results are discussed in this chapter.

Few reviews of the animal language training projects are not strongly biased one way or another. Those by Ristau and Robbins (1982) and by Ristau (1996) are exceptions, thoughtfully analyzing the methodology and results of all the early projects. Wallman's (1992) *Aping Language* is a useful but highly critical review of all the twentieth century work. *Kanzi, the Ape at the Brink of the Human Mind* (Savage-Rumbaugh and Lewin 1994) takes a somewhat different point of view.

15

Summing Up and Looking Ahead

In the few years since the first edition of this book was published, understanding of cognition in nonhuman species has been transformed by a plethora of new findings about animal memory, theory of mind, teaching, tool use, numerical cognition, imitation, social intelligence, communication, navigation, causal knowledge, and much more. These findings have been contributed by researchers with varying backgrounds and perspectives, with goals that range from learning how ants navigate in the desert to understanding how the human mind and culture evolved. Theory and data from animal cognition are becoming much better integrated with those from neighboring fields such as child development, primatology, behavioral ecology, cognitive neuroscience, and genetics. Such diversity within the field can be a source of conflict and controversy. For example, the proposal that that chimpanzees' or ravens' social competence reflects nothing more than exquisite sensitivity to cues from conspecifics' behavior may appear entirely reasonable to those trained in ethology or behavior analysis but strain credibility for anyone used to explaining behavior by invoking subjects' understanding of others. Similarly, referring to an ant leading another ant to food as teaching may be unproblematic to behavioral ecologists accustomed to classifying behavior functionally but profoundly questionable for anyone to whom *teaching* implies human pedagogy. Nevertheless, despite the inevitable attendant controversies, continuing engagement between researchers with such different perspectives is essential for the field's continuing progress and enrichment.

This chapter briefly revisits some of the issues introduced in Chapters 1 and 2 in the light of the material in succeeding chapters and reflects on some other issues that have emerged along the way. We begin by summarizing what Chapters 3–14 reveal about cognitive modularity and evolution and then look at some other overarching theoretical issues in the field, concluding with a question that goes right back to Darwin (1871), "Are human beings different from other animals in kind or only in degree?" Arguably this question has been at the core of comparative psychology ever since, but the many recent findings of unexpected competences in other species have inspired an outpouring of new attempts to answer it.

15.1 Modularity and the animal mind

15.1.1 Evidence for modularity: A quick summary

As evolutionary psychologists are fond of saying, the mind is like a Swiss Army knife, a general-purpose tool with many specialized parts. One defining property of a cognitive module is domain-specificity (Box 2.3): a given module processes a restricted kind of information in a functionally appropriate way but is impenetrable to other information. Chapter 3 provided some of the best evidence for modularity with the species-specific tuning of sensory systems. These examples from perception also show how *domain* is a fractal concept. Any category of environmental information can be infinitely subdivided into smaller and smaller nested domains: visual information, then color, shape, motion; spatial information, then vestibular motion sensations, visually localized landmarks, and so on. Deciding when we have more than one distinct cognitive module may depend on implicit assumptions about what differences are theoretically interesting.

Sherry and Schacter (1987) referred to cognitive modules, or memory systems to use their term, as having distinct rules of operation matched to environmental requirements for functionally incompatible kinds of information processing. To take their example, song learning (Chapter 13) and retrieving scatter hoarded food (Box 1.4; Chapter 7) must be subserved by different memory systems because in song learning a small amount of auditory information experienced repeatedly early in life is stored for months or years, whereas in food storing large amounts of briefly experienced spatial information are acquired and then forgotten throughout the bird's life. Such quantitative differences in amount and durability of information storage are not as strong support for cognitive modularity as are qualitative differences in how information is processed, stored, or used—different rules of operation in Sherry and Schacter's terms. Some examples come from explicit contrasts between two or more ways of processing superficially rather similar information. For instance, in Chapter 4 occasion setting (conditional control) was contrasted with the acquisition of excitation and inhibition. Chapter 8 presented evidence for a number of distinct spatial information processing modules, including path integration, the geometric module, the sun compass, and landmark use. Chapter 9 contrasted interval with circadian timing, Chapter 10 described evidence for two nonverbal number systems, and Chapter 13 discussed the distinct representational capacities presupposed by true imitation. The domains that define such candidates for separate cognitive modules are often more abstract than in the case of perception, where separate physical energies define domains. For instance, associative learning can take place with all sorts of inputs as long as they exemplify the abstract relationships typical of physical causation. Inputs can be tactile, visual, auditory, olfactory, and gustatory, and outputs can serve social, sexual, feeding, defensive, and other behavior systems, an example of a given modular ability supporting more than one adaptive use of information (Sherry 1988).

However, simply because of how the world works information acquisition has some general properties across multiple domains. For instance, although learning sometimes needs to be maximal after one trial—the ant or hamster that couldn't relocate its nest after a single trip on a unique path wouldn't survive to make other trips—in general the more often something has been repeated, the more likely it comes from a stable property of the world, worth remembering and responding to (Chapter 7). Hence, learning is rarely maximal after a single trial. How to combine information from multiple sources is another problem common to many domains, but it has a range of solutions. For instance, two weak physical causes of the same thing should produce an extra big response when they co occur, whereas cues for two different time intervals don't add up to a cue to respond at an extralong interval but to respond at each interval signaled, and two landmarks pointing to the same goal should lead to more precise localization of that goal. Blocking and overshadowing in associative learning are cases in which information from different sources is competitive, but we have also seen that different sources of information may be processed in parallel, treated as a unique configural entity, weighted in a Bayesian manner, or used hierarchically, with one giving conditional information about the significance of the other.

Discussions of modularity in cognition often emphasize that adaptive ways of processing different signals from the environment must be innate, like eyes, ears, and noses (Shepard 1994; Cosmides and Tooby 1994). Animals need an "innate schoolmarm" (Lorenz 1965), an “instinct to learn” (Marler 1991). There simply is not time in most animals' lifespans for appropriate ways of processing and using different kinds of information to develop from a system that is completely undifferentiated to start with. Prefunctional adaptive modularity is especially clear in sensory systems, in short-lived species like bees and ants, and in cases where learning has a crucial job to do early in life, long before correlates of its fitness consequences (as detected by evolved mechanisms of reinforcement) can feed back on cognitive organization. Imprinting (Chapter 5) and song learning (Chapter 13) are exceptionally clear examples of such early learning.

15.1.2 Modularity and cognitive evolution

The view that cognition is modular has implications for theorizing about cognitive evolution. On the traditional general process anthropocentric view (Chapter 1), species are ranked on a phylogenetic scale from simplest to most complex, and from less to more intelligent. Animal intelligence on this view consists of a hierarchy of learning processes (Macphail 1996; Thomas 1996; Papini 2002). Habituation, the most elementary, is shared by all species. Next in the hierarchy and of similarly wide generality is associative learning, then various forms of more “complex” learning and problem-solving, such as forming learning sets and acquiring abstract concepts. At the top of the hierarchy and unique to humans is language. But if instead intelligence is seen as solving problems of ecological relevance in the environment in which the species evolved, the question becomes what different species' intelligence consists of. Species differ in the number of states of the world they can discriminate—think of the difference between light-dark discrimination and color vision—and in the variety of ways they have available for acting on the world. For example the one-celled organism *Stentor* can ingest, reject, or escape things that come its way in an evolutionarily successful yet extremely simple manner (see Staddon 1983), but its cognition is undoubtedly less sophisticated than that of most vetebrates. Nevertheless, if cognition is modular we can expect that some abilities will be widely shared while others will appear only on a few branches of the evolutionary tree. Habituation and associative learning are examples of the former; true imitation appears to be an example of the latter. Language may be found in the human lineage alone.

A modular view of cognition is consistent with the suggestion that during evolution existing systems become accessible to a wider range of inputs (Rozin 1976; Heyes 2003). That is, they turn out to be exaptations, that is, evolved under one set of selection pressures but capable of being used to solve new adaptive problems (Sherry and Schacter 1987). For example, the hierarchical cognitive structure necessary for processing language may have evolved first in the context of social or spatial cognition (Chapter 14). Exaptation and accessibility may well be discernable in cognitive evolution, but it is important not to be too influenced by "boxes in the head" models of information processing like those depicted in Chapter 5 and elsewhere (Gallese 2007). For instance, associative learning is probably not localized to a single module in the brain that puts together any of a variety of inputs in the way described by the Rescorla-Wagner model and produces outputs appropriate to the behavior system being served. Rather it may be a general property of certain kinds of neural circuits regardless of the specific input-output systems they serve. On this view, accessibility or exaptation should be sought at the level of cellular or subcellular mechanisms (Papini 2002). That is to say, modularity may perhaps best be connected with evolution at the neurobiological or molecular level rather than at the level of functional cognitive modules such as numerical discrimination or associative learning (see Box 2.3; Barrett and Kurzban 2006).

In *The Origin of Species,* Darwin (1859) aimed to convince by sheer weight of evidence, by hundreds of examples from many phyla that all pointed to organic evolution. By contrast, there is very little systematic data on cognitive evolution. The two traditional approaches to biological species comparison (Hodos and Campbell 1969; Papini 2002) show the way forward: the adaptationist approach of comparing close relatives with divergent ecologies and the general process approach of comparing distant species to see whether processes are widely shared via a remote common ancestor (homologies) or independently evolved (i.e., homoplasies, examples of parallelism or convergence). When distantly related species show similar cognitive abilities, as in tool use or social cognition in corvids and apes, a key issue is how far the similarity extends. Functionally similar behavior in very different species may result from different neural, molecular, developmental and/or cognitive mechanisms (Papini 2002; Premack 2007). Thus research needs to go beyond simply testing whether some species or other demonstrates a particular competence. For example, comparison of tool using in captive rooks and bonobos in similar setups suggests that the cognitive underpinnings of the behavior are different in these two species (Helme et al. 2006.).

15.2 Theory and method in comparative cognition

15.2.1 Theory in comparative psychology

When Hodos and Campbell (1969) famously complained that "there is no theory in comparative psychology" they were referring to the fact that at the time many studies labeled "comparative" were mere "animal psychology" because they dealt with only a single nonhuman species. Comparisons were at most implicit and mostly with humans. Even more deplorable in their view, any comparisons that were made were referred to the phylogenetic scale rather than to real phylogenies. Hodos and Campbell were neither the first (see Beach 1950) nor the last (cf. Shettleworth 1993) to decry the shallowness of biological comparison in "comparative" psychology. But when it comes to comparative cognition in the early twenty-first century, the situation has changed dramatically. At least in most serious scientific literature, references to "higher" and "lower" or more and less intelligent animals have been replaced by discussion of convergences and divergences, abilities shared with common ancestors or more recently evolved, and the like. Increasing numbers of species are being studied, and increasingly two or more are compared within the same research program (Shettleworth 2009).

Of course explicitly comparative studies can still be distinguished from "animal cognition" research, but both are necessary components of an overarching enterprise, referred to in this book as research on comparative cognition (although perhaps cognitive ethology is more appropriate, Kamil 1998), aimed at understanding cognition across the animal kingdom, including how it works, what it is good for in nature, and how it evolved. In this context, in-depth studies of particular processes in one or a few species such associative learning in rats, visual category learning in pigeons, or social cognition in wild baboons are the foundations for well justified species comparisons. For example, comparisons of memory in food storing and nonstoring birds are built on method and theory developed largely in studies with pigeons that were based in turn on studies of human memory; comparisons of transitive inference in corvids with different social systems rest on method and theory developed with children, monkeys and pigeons.

Because analyses of single processes in a few species are as much a part of comparative cognition broadly construed as are explicit comparisons of multiple species, there is not *a theory* in comparative cognition, let alone comparative psychology more broadly, even though Hodos and Campbell's (1969) provocative title seems to imply there should be. Rather, there is a common framework consisting of modern evolutionary theory and Tinbergen's four questions within which explicit research questions are posed and data interpreted, whether to develop a theory of how a particular cognitive mechanism works or to understand species differences in terms of ecology and phylogeny. But there is another theoretical issue here: what exactly is being compared in comparative cognition? This is in effect a question of epistemology (Andrews 2007; 2009) or, more prosaically, of methodological approaches and pretheoretical assumptions. Unlike the form and occurrence of behavior patterns, cognitive processes cannot be observed directly. They are inferences from behavior, and the rules of inference in comparative cognition research are seldom explicit. Nevertheless, there are some fairly well accepted principles even if not universal agreement on their applications. Borrowing from Heyes's (2008) characterization of research on animal consciousness, we can say that contemporary research on cognition in animals deals with *functionally defined cognitive processes and states* studied with two methods: *analogical reasoning* and *experimental tests of alternative hypotheses.*

15.2.2 Functionally defined processes

To begin with, *functionally defined processes and states* refers to the assumption that in order to be a tractable subject for scientific investigation, cognitive processes in animals must be defined in terms of what they allow the animal to do, not how they feel, that is, what conscious mental processes accompany them. This functional approach is uncontroversial when applied to traditional topics in animal cognition such as associative learning, numerosity discrimination, timing, category formation. It is much more challenging when applied to aspects of cognition such episodic-like memory and metacognition that in humans are defined in part by the distinctive conscious processes that accompany them. Progress is greater in such research the better the process under study is defined and understood in humans. For instance

(Chapter 7), lack of consensus about the essential features of human episodic memory has encouraged multiple candidates for examples in animals, whereas research on animal metacognition has been focused on a well-defined set of nonverbal paradigms, paradigms which additionally can be used to test people in the same way as birds and monkeys. These paradigms also permit tests of functional similarities in the mathematical sense of relationships between independent variables such as retention interval or task difficulty and dependent variables such as proportions of correct responses. In contrast, some candidate demonstrations of animal episodic-like memory are limited by being pass-fail tests. Still, even well-accepted functional definitions of cognitive processes and rich comparative data sets do not always forestall debate about interpretations. Controversy most often arises in the case of processes understood mainly from introspection or folk psychology. Cognitive mapping, deception, planning, and understanding tools are examples. Even when, as with theory of mind, there are accepted experimental paradigms for human subjects, appropriate analogues for other species may not be obvious or straightforward.

15.2.3 Anthropomorphism and hypothesis testing

Analogical reasoning as a methodological approach (Heyes 2008) means using the venerable argument from analogy (see Povinelli, Bering, and Giambrone 2000)—in effect anthropomorphism—to infer cognitive processes. As with the nut-dropping crows at the beginning of Chapter 1, this means nothing more than inferring humanlike cognitive processes from humanlike behavior. Even if such inferences are convincing because the behavior in question is complex and observed in multiple situations, this method lacks explicit consideration and testing of alternative hypotheses. This approach was used extensively by cognitive ethologists such as D. Griffin (1978, 2001) and is still common in explanations of apparently complex behaviors in terms of conscious “higher” cognitive processes. For example, the chimpanzee putting its arm over the shoulders of the loser of a fight is empathizing and attempting to console, the scrub jay moving its caches to new locations understands the point of view of a competitor. But Morgan’s Canon dictates that we should entertain the cognitively “simplest” hypotheses possible. This usually means hypotheses grounded in knowledge of associative learning and/or species-typical behavioral predispositions. Unfortunately, it is not as widely known as it should be that associative learning can no longer be dismissed as especially simple or representationally impoverished. There is plenty of evidence (Chapters 4–6) that “mere associations” can encode events in the world with great subtlety and sophistication. Even bar pressing in “the humble rat” can express belief and desire (Chapter 11). Because associative learning is phylogenetically so widespread, it is generally the most reasonable null hypothesis in terms of evolution.

As elsewhere in science however, the most powerful method is experimental testing of competing predictions from alternative hypotheses. This method requires not only clear functional definitions but a good deal of imagination and general knowledge of animal learning and behavior besides. For example, how could a chimpanzee’s behavior in front of a mirror be explained other than by its having a self-concept? Maybe the chimpanzee is engaging in normal species-specific grooming behavior and neither the mirror nor the mark has anything to do with its touching the mark. How could a rat be finding its way without a cognitive map? Maybe the rat is using dead reckoning or comparing its present view of the environment to the view from its goal. Maybe a raven is not reading other birds’ minds but remembering it could see them when it was caching. Using imagination and background knowledge also means being aware that animals do not always see a testing situation as we do. From the animal's point of view, a test of theory of mind may be a conditioning experiment; a test of future planning may be exposure to cues that elicit species-typical ways of distributing food caches. The "simplest" explanations are not necessarily the simplest for us to imagine or introspect about (see Heyes 1998).

Explanations in terms of situation-specific behavior or learned responses can sometimes be tested with the experimental strategy of triangulation. Triangulation entails a series of tests designed to point to the same conclusion from different metaphorical angles. For example, an animal might be trained on an abstract concept in one set of conditions and then be given tests that are conceptually but not physically similar so that they cannot be solved by associative learning plus stimulus generalization. In some aspects of physical cognition, such as the Weber's Law–based number system, the same capacity has been demonstrated in each of several species using a variety of materials and behavioral measures. It can also be useful to ask whether it is reasonable to think that *X* has evolved rather than something cognitively simpler. What difference could it make to fitness for an animal to have conscious intentions, a theory of mind, a cognitive map, an explicit representation of a category prototype, or a concept of self? How could these come into play in the species' current natural environment or any plausible past one?

Of course formulating plausible alternatives, generating competing predictions, and devising incisive behavioral tests to discriminate them does not guarantee finding unambiguous answers. The capacity in question may be multifaceted, so species may differ in how many components of it they possess or in what situations they express them. As with numerical cognition, theory of mind, or language for example, the most productive approach to research and perhaps the most consistent with linking findings to evolution is to eschew questions like, "Do animals have capacity X or not?" and rather ask something like, "What are the components of X, and what species show them under what conditions?" Finally, no matter how clearly defined the methods, the power of the analogy between ourselves and other animals to determine the hypotheses researchers are willing to entertain about animal minds almost guarantees that the study of comparative cognition will continue to generate controversy.

15.3 Humans versus other species: Different in degree or kind?

Darwin's discussion of "mental powers" in Chapters 3 and 4 of *The Descent of Man and Selection in Relation to Sex* (Darwin 1879/2004) is one long argument that the human mind differs in degree but not in kind from the minds of other animals. Many of the findings described in this book clearly support his claim: when it comes to basic processes of perception, learning, memory, categorization, numerical discrimination, spatial orientation, and so on, other species do not differ from us in kind. But Darwin's claim has been getting renewed attention recently because of two sorts of new findings. On the one hand are the many observations of hitherto unsuspected humanlike abilities in species only distantly related to humans such as ants and birds. On the other are data from several productive groups whose research is specifically targeted at comparing human and ape (generally chimpanzee) cognition.

Ever since Jane Goodall described tool using and meat-eating in wild chimpanzees, the gap between humans and apes and even other species has often seemed to be getting smaller and smaller. One response to these developments (Premack 2007; Penn, Holyoak, and Povinelli 2008) is to emphasize that examples of animal teaching, tool use, culture, transitive inference, planning, and the like are profoundly different from analogous human behaviors. Many are highly domain-specific, perhaps relatively inflexible, species-typical behaviors with less complex cognitive underpinnings than their human counterparts. An ant, for example, can only "teach" another ant the route from nest to food. Humans are still unique, and the key to human uniqueness can be sought with comparative studies, primarily with apes but also with other animals. Such research asks the question, given that humans and chimpanzees are phylogenetically so close (cf. Hauser 2005), is there a "small difference that made a big difference" (Tomasello and Call 1997) to the human brain and cognition? How can cognitive differences between humans and other species best be characterized? Can this difference or differences be explained by hypotheses about the forces in hominid evolution? Can we ever pin it down genetically? And is there a single source of human cognitive uniqueness anyway?

15.3.1 On degrees and kinds

Darwin acknowledged that "the difference between the mind of the lowest man and that of the highest animal is immense" but "Nevertheless the difference in mind between man and the higher animals, great as it is, certainly is one of degree and not of kind" (Darwin 1879/2004, 150–151). Here Darwin refers to shared abilities such as memory that are developed to different degrees in different species. A second but confusingly similar sense of *degree* is implied by claims that the gap between the mind of man and other species is filled by "numberless gradations," that is, the human mind evolved by small degrees from the mind of some primitive ancestor. But even though evolution proceeds by tiny degrees over many generations, it can result in differences among organisms so great that they seem to be differences in kind. For example, snakes have evolved by degrees to leglessness, but snakes seem to be compellingly "different in kind" from lizards and crocodiles, not lizardlike reptiles that have legs to an infinitely small degree. When it comes to evolution of the human brain and cognition, we might expect to find apparent differences in kind from chimpanzees for the simple reason that there is not much evidence about the degrees by which we evolved from a common ancestor. All the species that could provide it are extinct. New evidence from fossil hominids may gradually fill this gap, as the discovery of dinosaur fossils with feathers helped to fill the gap between ancient reptiles and birds, but conclusions about "degrees" in cognitive evolution require in addition information about ancestral environments and behavior. Thus the relationship between characterizations of human—chimpanzee differences and human evolution is necessarily very speculative.

15.3.2 On sound species comparisons

Chapters 2, 6, and 7, among others, showed how rigorously comparing cognitive abilities across species requires taking into account a multitude of species differences in motivation, perception, developmental history, and other contextual variables. These important methodological caveats have largely fallen into the background in subsequent chapters even though research on single species reviewed in some of those chapters is implicitly comparative. Questions such as "do chimpanzees learn language?" or "do any primates imitate or cooperate?" generally mean "do they do it as humans do? “ But, as Christof Boesch (2007) has pointed out, most comparisons of apes and children, including recent explicit comparisons of children and chimpanzees, have failed to control for a number of serious confounds. As a result, any differences between apes and children in such studies may be explained by species differences in developmental history and/or the circumstances of the experiment rather than in the cognitive process under test. For example, even though there are cultural differences in human developmental trajectories and differences among wild populations of apes, not to mention vast differences in experience between wild and captive animals, middle-class Western children are usually compared with captive apes. The results may not generalize to children from other cultures and/or wild apes. Children are tested by members of their own species, and their mothers may be present if they are very young, whereas apes are usually tested by a member of a different species (humans), in a human-appropriate task, often while alone in a cage with the experimenter outside. Because most of these confounds seem likely to disadvantage the apes, they are especially problematical when the apes are found to lack an ability that the children show. They are also very difficult to avoid. Probably the best conclusion here is to be aware of the limitations of single studies (a warning that applies to any research comparing species) and work toward correcting them. A promising corrective to overemphasis on captive apes is research with chimpanzees and bonobos living in semi–free ranging colonies in Africa (see Hare 2007; Herrmann et al. 2007).

15.3.3 How and why are humans unique?

Two separate but related questions head this section. The first is, how can the apparent cognitive uniqueness of humans be characterized? Answering it entails comparing present-day humans with other present-day species, most often chimpanzees, and trying to distill the catalog of findings into some key difference or differences. We look briefly at three contemporary efforts to do this. The second question is, what explains how any proposed key difference(s) evolved? Answering it entails speculating about circumstances early in hominid evolution and how they might select for one or another human ability.

Language

Candidates for uniquely human aspects of cognition mentioned in this book include understanding the minds of others and how tools work; domain-general abilities to form abstract concepts, make transitive inferences, plan, and teach; imitation; precise discrimination among quantities greater than four; cumulative culture; reflective consciousness; and above all, language. Indeed, the possession of language is a time-honored explanation for all other uniquely human cognitive abilities. Undoubtedly language is used in expressing most forms of human understanding, but when it comes to going beyond characterizing how humans differ from all other living species to explaining how the critical difference or differences evolved, language encounters a classic chicken-and-egg problem. Why would complex language evolve in a creature that did not already have the concepts it requires or expresses? Many comparative psychologists (cf. Terrace 1984; Watanabe and Huber 2006) might claim that research with other species can reveal the nature of thought without language. If so, those thoughts are relatively simple. One possibility is that language and thought coevolved, ratcheting each other up as language created a new “cognitive niche" (A. Clark 2006). However, this viewpoint still assumes that a key difference between present-day humans and apes is language, and not everyone agrees. For one thing, if language ability itself is the product of multiple adaptations (Pinker and Jackendoff, 2005), human uniqueness must be sought in specializations of many distinct modules. This possibility has not, however, prevented two groups of researchers from proposing and testing rather sweeping characterizations of human cognitive uniqueness.

Shared intentionality

According to Tomasello and his colleagues (Tomasello et al. 2005; Hare 2007; Moll and Tomasello 2007) the primary difference between present-day humans and chimpanzees is not essentially cognitive but motivational: only humans are motivated to communicate about and share intentions in "cooperative communicative interactions." Examples of what this means can be found throughout the discussions of theory of mind and cooperation in Chapter 12 Chimpanzees are good at competing with others but poor at cooperating. In competitive interactions, they are sensitive to cues associated with another's intentions, a sensitivity which Tomasello and colleagues (e.g., Tomasello et al. 2005) controversially interpret as "understanding intentions," but fail to exhibit such sensitivity in situations where children readily cooperate. Further evidence comes from perhaps the largest single comparative experiment ever reported (Herrmann et al. 2007), in which each of 106 chimpanzees, 32 orangutans, and 105 2.5-year-old children was given a large battery of tests of physical and social cognition. Notice that the children were at an age before they had developed extensive language or had formal schooling. The apes lived in sanctuaries in their native countries. The tests of physical cognition included simple tests of spatial memory (e.g., for the location of a reward on a table), numerical competence (e.g., choosing the larger of two quantities), and tool use (e.g., using a stick or choosing an unbroken cloth to pull in a reward). Tests of social cognition included following gaze, using communicative cues such as pointing, and imitating simple tasks such as shaking a reward out of a tube. As shown in Figure 15.1 by summaries

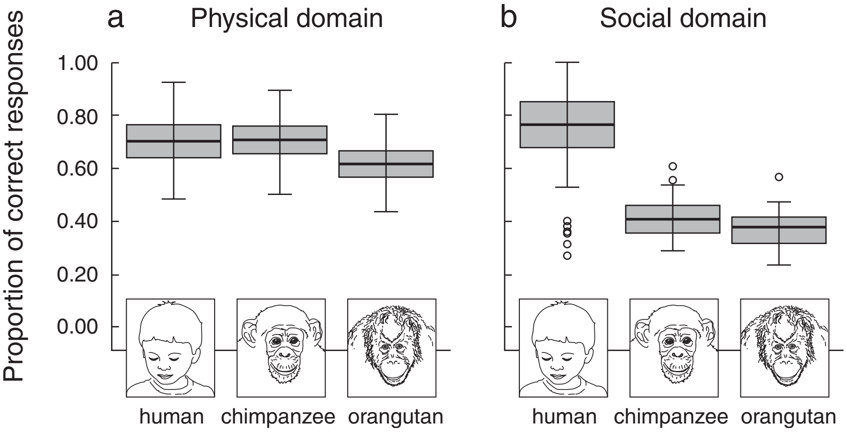


Figure 15.1. Mean performance of three primate species on a battery of tests of physical and social cognition. Open dots in these box plots represent outliers. Redrawn from Herrmann et al. (2007) with permission.

across all tests within each domain, on average children and apes performed similarly on the tests of physical cognition, but the children did substantially better on the tests of social cognition. The species difference was most marked in the tests of imitation, which many of the apes failed altogether, but it was found in the other tests of social cognition as well.

Although this study is not entirely free of the problems with ape-human comparisons outlined in Section 15.3.2 (de Waal et al. 2008) it does provide impressive support for "the cultural intelligence hypothesis" (Moll and Tomasello 2007). On this hypothesis, the unique social skills and motivation that humans have from an early age are the scaffold for developing other uniquely human cognitive skills. It can be seen as consistent with the social brain hypothesis discussed in Chapter 12, in that social systems rather than foraging specializations may have driven the evolution of primate intelligence, but goes beyond it to suggest that conditions in human society uniquely selected for new and intense forms of cooperation. On this scenario, language evolved in the context of motivation to share thoughts in the service of cooperation. It should be noted, however, that even the original authors of the ape-child comparison (Herrmann et al. 2007, 4365) acknowledge that comparatively poor physical dexterity may have disadvantaged the children in some of the physical tests, leaving open the possibility of a domain general difference such as that discussed next.

Relational reinterpretation

In contrast to the "cultural cognition" hypothesis, Penn, Holyoak, and Povinelli's (2008) "relational reinterpretation" hypothesis proposes that only humans have a domain-general ability to represent abstract relationships, or to reinterpret perceptual (or first-order) relationships in terms of higher-order relationships. This is essentially an extension of the earlier claims of Povinelli and colleagues (e.g., Povinelli 2000; Vonk and Povinelli 2006) with respect to tool use and theory of mind. Recall, for example, that the chimpanzees in Povinelli's (2000) experiments could choose effective tools on the basis of perceptible cues but showed no evidence of the sort of reasoning about unobservable causes that could help them with new tools or situations. Similarly, chimpanzees as well as scrub jays and ravens are very good at using subtle social cues to deceive, compete, and so on, but on this account such behavior is not mediated by a representation of other individuals' mental states. Penn, Holyoak and Povinelli (2008; see also Premack 2007) also analyze further examples from chimpanzees and other species to argue that animal behaviors that qualify as teaching, planning, transitive inference, causal reasoning, or the like are always confined to narrow domains and highly specific cues. Only humans, on their account, can represent abstract or higher-order relationships in a domain-general way. Clearly in normal adult humans this ability is expressed in language, but on this account it does not require language, although language and the ability to represent higher-order relationships may well have evolved together, scaffolding each other up.

Conclusions

This section has concluded with a bare sketch of two prominent contemporary proposals for the nature and evolution of human cognitive uniqueness, both of which are far more detailed and nuanced than can be conveyed in a short summary. The cultural cognition hypothesis is primarily motivational and domain-specific, whereas the relational representation hypothesis directly addresses cognition. It proposes a domain-general ability that cuts across all the domain specific cognitive processes documented in this book, in the process encompassing the species differences in social cognition found by Herrmann and colleagues (2007). Thus it poses interesting questions about cognitive architecture and evolution, such as how it could be compatible with the modular view of cognition. The cultural cognition hypothesis has the attraction of being easily linked to current notions about the evolution of human society and culture (cf. D. Wilson and Wilson 2007; Gintis et al. 2007) whereas the relational reinterpretation hypothesis seems to capture very well what is special about human thought. Both could be correct to some extent, and in any case it seems unlikely that any single global characterization of human-nonhuman cognitive differences will embrace everything from imitation to higher mathematics to imagining the future. What we can expect, given the explosion of relevant research on comparative cognition together with the promise of comparative genome projects and cognitive neuroscience to reveal the molecular bases of species differences, is continued debate about the degrees and kinds of differences between human and animal minds.

15.4 The future: Tinbergen's four questions, and a fifth one

Introductions to animal behavior for biology students traditionally begin by defining Tinbergen's four questions—cause, function, evolution, and development—and go on to emphasize that they must not be confused with one another (Chapters 1 and 2). Particularly insidious is the ease with which cause can be confused with function and functional answers given to causal questions. For instance, a plover's broken-wing display (Box 12.1) may function to deceive a fox, in that the fox responds as he would to an injured bird, but this does not mean that the plover intends to deceive or that the fox is consciously thinking the bird is injured and would therefore be easy prey. During the last 30–40 years, the tendency to such confusions has been exacerbated by theoretical developments in both the biology and the psychology of animal behavior. With the rise of behavioral ecology in the 1970s, traditional ethological causal analyses in terms of sign stimuli, fixed action patterns and the like seemed increasingly old fashioned and theoretically uninteresting (Dawkins 1989). The answer to "what is this animal doing?" was more likely to be "attracting a mate" than "bowing and cooing in response to cues from a female." As a result, students were not always taught to look at behavior qua behavior. In addition, many terms used by behavioral ecologists such as *sampling, optimizing,* and *deceiving* easily slip into use as causal explanations because they have both functional and folk-psychological interpretations (Kennedy 1992).

At more or less the same time as traditional ethology was becoming less popular, the shift within experimental psychology from behaviorism to cognitivism meant that psychology students were not so often exposed to behavior analysis as a valuable aid to causal understanding. Explaining behavior as the expression of memories, concepts, representations, and the like seems to preclude explanation in terms of observable factors such as past history and present cues. But just as Tinbergen emphasized keeping all four questions in mind and seeking to answer them in an integrated way, so it is important to know about and keep in mind alternative ways of answering causal questions.

Consider, for example, the history of research on theory of mind in chimpanzees. One of the earliest experiments was taken to show that chimpanzees understood another individual's knowledge or ignorance because they begged from a knowledgeable individual on more than 50% of novel test trials (see Section 12.4.2). A challenge from a learning theorist (Heyes 1993b) led to examination of trial-by-trial data and supported the conclusion that instead the animals had learned to choose correctly during the test phase itself (Povinelli 1994). Here what can be seen as a test of theory of mind is at the same time an occasion for simple discrimination learning. More recent developments in research on animal theory of mind have further deconstructed the original tests to characterize the cues and responses that come into play in more detail. We have seen experiments testing the role of human versus chimpanzee partners, competition versus cooperation, and a history of selection for responding to humans. Whether such studies have clarified the nature of chimpanzee theory of mind or made the notion unnecessary is a matter of debate, but either way looking closely at causes of the animals' behavior as such is essential.

The importance of becoming aware of and then keeping in mind multiple levels and kinds of explanation is perhaps no better illustrated than by the evolution of research on optimal foraging and choice discussed in Section 11.1. Research on choice that began as tests of optimal foraging models, that is, designed to answer functional questions, was soon seen to be measuring behavior on schedules of reinforcement, and the results therefore demanded causal interpretation in the light of an extensive psychological literature. And because many of the situations studied involved rewards distributed through time, the growing literature on the properties of timing became relevant. In turn, some findings from experiments designed to mimic foraging situations fed back on and modified causal accounts of instrumental learning and choice. And in the most recent research, all of these findings are being interpreted in the light of economic models of choice and decision making, in effect comparing predictions from contrasting notions of rationality (Kacelnik 2006). Such developments suggest that to Tinbergen's four questions should be added a fifth one: What do alternative perspectives have to say about this behavior and how can they be integrated?

In conclusion, research on cognitive processes in animals is thriving in the early twenty-first century, embracing research from behavioral ecology to cognitive neuroscience, in the field and the experimental psychology laboratory, on species from ants and honeybees to chimpanzees and people. The range of topics being studied is probably more comprehensive now than at any other time since Darwin (1871) marshaled his evidence for animal minds, embracing mechanisms of physical and social cognition in equal measure with domain-general learning and memory processes. Research on nonhuman species is increasingly integrated with research on humans. Parallel experiments on multiple species are designed to test species-general theories of specific mechanisms, and comparative data are brought to bear on theories of how the human mind evolved. Evolution and function are considered in a more sophisticated way than in the past, and individual research programs increasingly address more than one of Tinbergen's four questions. Much of the diversity of subjects and approaches reflects the diversity of researchers' backgrounds. Although this is sometimes the source of misunderstanding and controversy, it has greatly enriched the field and undoubtedly will continue to do so.

Further reading

Barrett and Kurzban (2006) is the best source for a balanced discussion of the many facets of modularity. Darwin's (1871) chapters on "Mental powers" and "Moral faculties" are still thought-provoking, but the best route to a full sense of the richness and depth of contemporary discussions about the nature of human cognitive uniqueness is to read the articles by Tomasello et al. (2005) and Penn, Holyoak and Povinelli (2008) together with their associated commentaries. Premack (2007) is a short and pithy critique of recent claims to demonstrate humanlike abilities in other species.

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