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The Evolution of Communication

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1 Synopsis of the Argument

1.1 General Comments

Nothing would work in the absence of communication. Flowers must communicate with bees in order for pollination to be successful. Male songbirds must communicate with females if they are to mate and rear young. Lions on a cooperative hunt must communicate with each other about how they will attack their prey. A human infant must communicate with its parents so that the needs of both are met. Great orators, such as Jesse Jackson, must use their communicative skills to captivate and manipulate the emotions of their audience. Computer programmers must design software to communicate with their hardware. And who knows, perhaps there are extraterrestrials trying to communicate with us at this very moment, although perhaps more successfully with some of us mere mortals than with others.

But why do birds sing rather than speak Mandarin? Why don't human infants scream and cry when they are content as peas in a pod, but coo and gurgle when they are angry, annoyed, or in pain? And why doesn't Jesse Jackson simply convey his expressive skills by blinking his eyes, Morse code style? These are questions about design, and what is true of all communication systems that work is that they have specific design features. The design features of a communication system are the result of a complex interaction between the constraints of the system and the demands of the job required. Consider the traffic light. There are two sorts that I am aware of. The old-fashioned ones consist of red, yellow, and green lights that can be seen at any distance, but have the disadvantage that they are difficult to detect in bright sunlight. The newfangled ones often look as though they are dead when seen at a distance, but come to life when approached, regardless of lighting conditions. Thus both morphs have been designed to convey specific information about the flow of traffic, and the advantages and disadvantages of each relate to the constraints of the technology. For natural communication systems, such as those observed in the plant and animal kingdoms, constraints can be seen at several levels including neurobiological, physiological, and psychological. These constraints are important, for they determine the relative success of the organism in responding to socioecologically relevant stimuli in the environment.

This book is about the evolution of communication. For all organisms, including humans, communication provides a vehicle for conveying information and for expressing to others what has been perceived. But organisms differ with regard to what they can convey and what they can perceive. Consequently, there are a diversity of communication systems in the natural world, and I hope to shed light

on the causal factors that have been responsible for the evolution of such diversity. To accomplish this goal, we require a comparative perspective that tackles the variation in communication forms head-on. In this book, therefore, I follow the ethologist—Nobel laureate Nikolaas Tinbergen (1952) and explore the diversity of animal communication systems from four perspectives. These perspectives, I believe, provide the only fully encompassing and explanatory approach to communication in the animal kingdom, including human language:

1. *Mechanistic* Understanding the mechanisms (e.g., neural, physiological, psychological) underlying the expression of a trait.
2. *Ontogenetic* Determining the genetic and environmental factors that guide the development of a trait.
3. *Functional* Looking at a trait in terms of its effects on survival and reproduction (i.e., its fitness consequences).
4. *Phylogenetic* Unraveling the evolutionary history of the species so that the structure of the trait can be evaluated in light of ancestral features.

These perspectives or problems are not hierarchically structured. They represent a coherent theoretical and methodological framework for both studying and explaining communication. Although researchers may prefer to work on some problems and not others,¹ variation can only be fully explained when comprehensive answers to all four issues have been addressed (for a recent discussion of the interaction between causal and functional analyses, see Alcock and Sherman 1994; Curio 1994).

Perhaps the most exquisite testimony to the success of Tinbergen's framework comes from the study of birdsong, where observations and experiments have addressed questions of mechanism, ontogeny, function, and phylogeny (Konishi et al. 1989).² In brief, detailed neurobiological studies have revealed dedicated neural pathways underlying song production and perception, and in many species such pathways and their associated nuclei are sensitive to changes in circulating

1. When the fields of sociobiology and behavioral ecology emerged in the 1970s, many researchers restricted their analyses to problems of function or ultimate causation. Although this restriction continues to characterize a good deal of work in behavioral ecology, an emerging trend in studies of animal behavior is to revert to the Tinbergian prescription, integrating studies of function with studies of mechanistic causation, ontogeny, and phylogeny. An elegant example of such integration, discussed in greater detail further on in the book, is Michael Ryan's studies of vocal communication in frogs.

2. The discussion here is intentionally brief and general. A more complete account of within- and between-species variation in birdsong is provided in chapters 4 to 7.

hormones. Ontogenetically, song develops gradually over time, constrained in part by species-specific auditory templates and shaped by acoustic features of the environment, both social and ecological. Studies of wild birds indicate that song serves at least two important functions—territorial defense and mate attraction—and females commonly use song to guide their mating decisions. In terms of phylogeny, not all birds sing, and among those that do, there is considerable variation in structure even among closely related species. In sum, therefore, current understanding of birdsong far exceeds many other areas of animal behavior because the question “Why?” has been addressed from the four Tinbergian perspectives.

A close look at what we know about human language suggests that our understanding of mechanism and ontogeny is sophisticated (see chapters 4, 5, and 7), whereas our understanding of function and phylogeny is relatively poor.³ In fact, rarely have researchers asked whether language should be considered an adaptation⁴ (for important exceptions, see Lieberman 1984, 1991; Pinker and Bloom 1990; Pinker 1994a) and, if so, what its fitness consequences are for members of the species (Cheney and Seyfarth 1990; Dunbar 1993). There are at least four reasons for this omission, which I develop only briefly here (see chapter 2). First, for some linguists, the analytical lens focuses exclusively on the problem of syntax. Those working on this aspect of language show little interest in the fact that syntactic structure provides humans with an extraordinary communicative tool and, as a result, show little interest in the evolutionary pressures that may have led to this form of communication rather than some other form. Second, language is sometimes conceived as a trait that is detached from our biology—most of the interesting features of language are the result of cultural processes. Clearly, anything that is not part of our biology cannot be an adaptation, *sensu strictu*. Third, interest in the evolutionary origins of language has concentrated

3. By the phylogeny of language, I am referring to the evolutionary changes in communicative structure and function preceding the emergence of language in modern humans (i.e., *Homo sapiens sapiens*), rather than historical changes in linguistic form following the emergence of modern humans (for a recent, nontechnical review, see Ruhlen 1994).

4. I am using the term *adaptation* to mean a trait that evolved in response to a particular socioecological problem, where the design features of the trait can be shown to be causally related to the individual's probability of survival and reproductive success; such features represent the best solution to the problem out of a number of possible solutions. In this sense, my use of *adaptation* is similar to the one proposed by Reeve and Sherman (1993), and different from those who consider trait history to be important (S. J. Gould and Vrba 1982). For those interested in phenotypes and their fitness consequences, history is important (Lauder, Leroi, and Rose 1993), but current design features and functional utility are more relevant to the problem at hand. These ideas are more fully developed in chapter 3.

on syntax and the computational machinery that it appears to require. In some accounts, such as Chomsky's (1986), the machinery is considered a unique feature of modern humans. Without precursors, it makes little sense to talk about gradual evolution by natural selection. Last, evolutionary thinking has generally played a minor role in the social sciences. This statement is certainly true of most researchers working on human language, with a few notable exceptions (e.g., Fer-nald 1992b; Kuhl 1989; Lieberman 1991; Locke 1993; MacNeilage 1991, in press; Pinker 1994a; Pinker and Bloom 1990; Studdert-Kennedy 1981, 1991). In sum, the study of human language requires a good dose of Tinbergen's medicine, and especially, medicine flavored with functional and phylogenetic ingredients.

To set up the argument I will develop in this book, let me start with a few distinctions that are critical to a sophisticated comparative analysis.⁵ First, it is important to distinguish between phylogenetic analyses that consider the evolutionary history of a trait, and adaptationists' analyses that consider how a trait contributes to an individual's survival and reproductive success. Thus, if one were interested in the phylogenetic origins of mating signals, one might approach this problem by looking within a narrow range of organisms (e.g., comparing song structure among Passerine species; see Read and Weary 1992) or from within a relatively more expansive range, comparing distantly related species (e.g., contrasting the displays used by insects and birds in the context of lek mating; Brad-bury 1985). The goal here is to quantify the structure of a signal (e.g., its defining features) and then determine when, evolutionarily, the signal first appeared within a group of organisms. For this kind of analysis to succeed, however, a phylogeny is required, based on nonvocal characteristics such as genetic sequence data (nuclear or mitochondrial) and morphological measurements of relevant anatomical traits. In addition to addressing the phylogenetic problem, one might further examine whether a particular mating signal is an adaptation by documenting how it contributes to an individual's genetic fitness. Thus one might examine whether variation in mating success can be accounted for by variation in signal structure. For example, in a species where females choose mates on the basis of their advertisement calls, do males with low-pitched vocalizations obtain more matings than males with high-pitched vocalizations?

Research on communication has tended to adopt a relatively narrow comparative approach with regard to the range of species explored (for some important

5. For a general discussion of issues in comparative biology, see Ridley's (1983) introductory text. More specific and technical details are provided in Harvey and Pagel (1991). I develop some of these issues in section 1.2.2.

exceptions, see Marler 1955, 1967, 1977; W. J. Smith 1977), and I believe this narrow range has hindered our understanding of the evolution of communication systems. In the absence of broad taxonomic comparisons, it is difficult to assess both the adaptive significance and phylogenetic history of a trait, either in terms of homology or homoplasy.⁶

My approach in this book, therefore, is to provide a framework for studying communication from a broad comparative perspective, using both closely and distantly related species to inspect how adaptive solutions to specific problems have evolved. This project requires a synthesis of existing data and theory together with an attempt to provide general methodological tools that can be used with a wide diversity of species. Needless to say, I cannot hope to provide a complete solution. I believe, however, that the synthetic approach adopted here will lead to new insights, that broad-spectrum methodological techniques are available, and that, with a bit of effort, these can be readily implemented into the study of a taxonomically diverse group of organisms.

The empirical work reviewed is restricted to natural communication systems that use auditory, visual, or audiovisual signals. There are two reasons for this restriction. First, by focusing on taxonomic groups that use either auditory or visual signals, we open the opportunity to explore homologous as well as homoplastic traits for a substantial set of species, thereby enriching the power of the comparative approach. Although a considerable amount of work has been conducted on other signaling modalities, including chemical, tactile, and electrical, adding on these modalities would cause some taxonomic groups to be overrepresented and others to be underrepresented. This is especially the case for electrical signaling, where studies of fish far exceed all other animal groups. Additionally, because human language is communicated via auditory and visual channels,⁷ the design features of our own communication system can be directly compared to the design features of other animals without the complications of different sensory

6. For those less familiar with this distinction, a simple and succinct discussion can be found in Hodos and Campbell (1990). In brief, homoplasies represent traits that are similar and have evolved independently in two distantly related taxonomic groups. Homoplasies commonly arise from convergent evolution, a process that results from the fact that when two species confront similar ecological problems, selection typically provides similar solutions. In contrast, when a trait is similar in two taxonomic groups as a result of shared evolutionary ancestry, then the trait is considered homologous. In general, traits that are functionally significant with regard to survival and reproduction tend to show up in the evolutionary record in a wide variety of distantly related taxonomic groups. As a result, such traits tend to be convergent or homoplastic. See discussion in section 1.2.2.

7. Although other sensory modalities may provide additional communicative information (e.g., chemical signals that influence the menstrual cycle; McClintock 1971) and tactile signals used by the blind and deaf (e.g., the Tadoma method; Vivian 1966), the auditory and visual channels are primary.

modalities. Second, I focus on natural communication systems, excluding research on nonhumans who have been taught a novel or artificial system. What we have learned from the latter studies is both impressive and clearly of importance in any discussion of comparative cognition. In this book, however, I am primarily concerned with communication systems that evolved in response to naturally occurring problems in the species-typical environment.

1.2 Some Background Information

1.2.1 Communication and Information

Almost every author who has written on the topic of communication has provided a working definition, and as several analyses reveal, it is not an easy task (Mellor 1990). Definitions are interesting for at least two reasons. They provide information on the particular theoretical slant of the author and typically serve as guiding (constraining?) forces in empirical investigations. Table 1.1 provides a sample of definitions of communication from researchers in sociobiology, behavioral ecology, sensory ecology, neuropsychology, cognitive psychology, and linguistics—disciplines with a major representation in this book.

The concepts of *information* and *signal* form integral components of most definitions of communication, including the ones listed in Table 1.1. Both concepts are associated with long lists of operational definitions. Because this is a book about communication between organisms, my bias is to couch information and signal in terms of their functional design features. Thus information is a feature of an interaction (i.e., not an abstraction that can be discussed in the absence of some specific context; see Box 1.1) between sender and perceiver. Signals carry certain kinds of informational content, which can be manipulated by the sender and differentially acted upon by the perceiver. Signals have been designed to serve particular functions, and the functions they serve must be evaluated in light of both production and perception constraints. Thus the stomatopod *Gonodactylus bredeni*, a small marine shrimp, defends its nest cavity with a visual display that involves either a simple extension of its powerful cheliped (i.e., claw) or an extension and ground strike (Caldwell and Dingle 1975). Potential competitors can either accept this aggressive signal at face value and retreat, or challenge the cavity owner by intruding further.⁸ Constraints on the system include the ener-

8. As discussed in chapters 6 and 7, Caldwell's (1986) elegant experiments on this stomatopod reveal that this system is extremely plastic, and even suggest the possibility of cavity owners sending dishonest information in the form of a functional "bluff."

Table 1.1
Definitions of Communication: A Sampler

Authors (discipline)	Definition
Wilson (1975) Sociobiology	"Communication occurs when the action of or cue given by one organism is perceived by and thus alters the probability pattern of behavior in another organism in a fashion adaptive to either one or both of the participants" (p. 111).
Hailman (1977) Ethology	"Communication is the transfer of information via signals sent in a channel between a sender and a receiver. The occurrence of communication is recognized by a difference in the behavior of the reputed receiver in two situations that differ only in the presence or absence of the reputed signal. . . . the effect of a signal may be to prevent a change in the receiver's output, or to maintain a specific internal behavioral state of readiness" (p. 52).
Dusenbery (1992) Sensory ecology	"The term 'true communication' is restricted to cases in which the transmitting organism engages in behavior that is adaptive principally because it generates a signal and the interaction mediated by the signal is adaptive to the receiving organism as well" (p. 37).
Krebs and Davies (1993) Behavioral ecology	"The process in which actors use specially designed signals or displays to modify the behaviour of reactors" (p. 349).
Kimura (1993) Neuropsychology	"The term is used here in a narrower sense, to refer to the behaviors by which one member of a species conveys information to another member of the species" (p. 3).
Johnson-Laird (1990) Cognitive psychology	"Communication is a matter of causal influence. . . . the communicator [must] construct an internal representation of the external world, and then . . . carry out some symbolic behaviour that conveys the content of that representation. The recipient must first perceive the symbolic behaviour, i.e. construct its internal representation, and then from it recover a further internal representation of the state that it signifies. This final step depends on access to the arbitrary conventions governing the interpretation of the symbolic behaviour" (pp. 2-4).
Lindblom (1990) Linguistics	"Human communication . . . includes forms of verbal communication such as speech, written language and sign language. It comprises nonverbal modes that do not invoke language proper, but that nevertheless constitute extremely important aspects of how we communicate. As we interact, we make various gestures—some vocal and audible, others nonvocal like patterns of eye contact and movements of the face and the body. Whether intentional or not, these behaviors carry a great deal of communicative significance" (p. 220).

Box 1.1 The Statistical Theory of Information

Although the computer generation has dramatically improved the flow of information, there is still no generally accepted definition of *information*. Nonetheless, a commonly used framework, proposed by Shannon and Weaver (1949), is the statistical or mathematical theory of information; in addition to engineers, the implications and applications of this approach have been discussed by biologists (e.g., Fagen 1978), psychologists (Attneave 1959), and philosophers (Dretske 1981). In simple language, Shannon and Weaver proposed that the function of information is to reduce the observer's uncertainty about a particular event. For example, imagine a boxing match between two heavyweight contenders; let's call them George and Michael. Before the match, each knows a bit about the other's boxing talents based on fighting records and, perhaps, observed fights. In this sense, George and Michael have information, and their uncertainty about the outcome of the fight is clearly nonzero. When George and Michael enter the ring and take their respective corners, they gain additional information. George is older than Michael and looks tired, but is acting cocky. Michael refuses to make eye contact, looks cool and collected, and is in great physical shape. The bell rings, and George comes flying out and swings wildly at Michael, missing. More information. At each step of the interaction, therefore, there is some reduction or change in uncertainty, and this can be formalized by the following equation:

$$H(X) = - \sum_{i=1}^k p_i \log_2 p_i$$

Here, X designates a set or field of events x_i to x_k (e.g., walking into the ring, throwing a punch, etc.), and p_i stands for the probability that the i^{th} event of set X will occur. This formalization can be used to assess (1) the extent to which a receiver's uncertainty is reduced by the transmission of the sender's signal and (2) in cases of two or more interacting individuals, whether communication has occurred. Regarding the latter, the goal of the Shannon-Weaver approach is to determine whether the type of response selected by the receiver appears to be causally related to the type of signal selected by the sender. More complete treatments of these issues, as they relate to natural communication systems, are provided by Markl (1985), Dusenbery (1992), and Allen and Hauser (1993).

genetic costs associated with generating the chiliped display and the ability of the intruder to properly perceive the display given its visual system⁹ and the channel in which the signal was conveyed.

We tend to think of biological signals as conveying or carrying information. In general, this characterization is accurate. For purposes of clarity, however, I will

9. Interestingly, stomatopods have highly mobile eyes that look like translucent crystal balls sitting upon rotating stalks (Cronin and Marshall 1989). This mobility has presumably been designed to provide cavity owners with the potential to scan in all directions without having to move outside of the cavity. In addition to their mobility, recent neurobiological studies have revealed that the stomatopod visual system consists of eight cones, thereby providing a potentially exquisite system for detecting subtle difference in color among conspecifics. Such fine-grained discriminations may be extremely important given the potentially lethal consequences of aggressive interactions—a single strike with the claw can result in immediate death.

draw a technical distinction between *cues* and *signals*. Cues, like signals, represent potential sources of information. Cues, however, differ from signals in two important ways.¹⁰ First, cues tend to be permanently ON, whereas signals are more plastic and can be in an ON and OFF state. As a result, signals, but not cues, are produced in response to socioecologically relevant and temporally varying changes in the environment. Second, cues typically correspond to an individual's or species' phenotype, and their expression carries no immediate extra cost. Signals, although individual- and species-specific, are associated with significant costs of expression. Thus, for example, a number of poisonous species have distinctive warning colors (Guilford 1989a, 1990; see chapter 6). These colors are cues. They are permanently ON, they are part of the individual's phenotype, they require no extra cost to produce, and they have been designed to be informative. In contrast, several avian and mammalian species produce warning calls in response to predators. Such calls can be turned ON and OFF (e.g., whether or not an animal calls is mediated by changes in the social environment; Marler, Karakashian, and Gyger 1991), they are costly to produce, and they have been designed to be informative (Marler 1955).

A second distinction is necessary between signals and cues on the one hand, and what I will call *signs*.¹¹ Cues, such as sexual ornaments and warning colors, have been selected to be informative, and such information can be extracted directly from the individual. For instance, in several avian species, females appear to use tail length as an accurate predictor of male fitness (e.g., Andersson 1982; Møller 1988b, 1989, 1993). Tail length,¹² as a cue, is likely to be an accurate predictor because maintaining this trait is costly. Signs, in contrast to cues, are either temporally or spatially displaced from the individual and are informative to perceivers¹³ as a result of their association with biologically significant features of the environment. For example, several species construct nests for raising their young (e.g., birds) or for rest (e.g., chimpanzees). Among birds, parasitic species (e.g., cowbirds) require mechanisms for recognizing potential hosts, and it is possible that the species-specific architecture of the nest is a relevant piece of

10. I recognize that some exceptions to this generalization may exist. I leave the subtlety of the distinction between cues and signals for later chapters.

11. The use of the word "sign" here has little to do with its implementation in semiotics.

12. As discussed more thoroughly in chapter 6, tail length is commonly viewed as a sexually selected trait, exaggerated in males relative to females. In some species, females preferentially mate with males who have long tails.

13. What may be a sign to a perceiver could very well be a signal for a sender. Thus advertisement calls produced by male frogs would be signals to female frogs, but from the perspective of a predatory bat, they are signs.

information. Similarly, forest monkeys could use chimpanzee nests to avoid predation, though this hypothesis has never been formally tested. In these situations, nests become informative (i.e., they acquire predictive power) because of specific environmentally relevant associations. They have not, however, been designed to be informative in this specific way. To hammer the distinction home, consider the tracks left by predatory species such as lions and pythons. As a result of their locomotory patterns and their frequent travels through dusty soils, these species leave traces of their presence. A "smart" prey species might learn that particular traces are associated with danger whereas other traces are not. Clearly, lions and pythons do not intend their traces to be informative. From the prey's perspective, however, they would represent informational bonanzas, signs of potential danger.

The distinction between signals and cues is not novel (see, for example, Markl 1985; Seeley 1989; Dusenbery 1992). However, my own characterization of the distinction differs from previous authors in one crucial way. To illustrate, consider Seeley's (1989) succinct account (p. 547): "Signals are stimuli that convey information and have been molded by natural selection to do so; cues are stimuli that contain information but have not been shaped by natural selection specifically to convey information." In contrast to Seeley, I suggest, and will empirically substantiate further on, that both signals and cues have been designed to convey information, but signs have not. Most of the communication systems discussed in this book involve signals, rather than cues or signs.

1.2.2 The Comparative Method: Which Species to Compare and What to Conclude?

In addition to his theory of natural selection, the comparative method is what made Darwin great. If you don't believe this claim, look at any of his major works. They are packed with interspecific comparisons based on detailed studies and anecdotal observations. As previously mentioned, however, studies of communication have generally compared closely related species. What is sorely needed is for communication to be treated on a broader phylogenetic scale. For this effort to succeed, however, we require methods that will generate comparable data and statistical techniques that will allow us to properly interpret evolutionary relationships. At present, there are few methodological tools that can be treated as species-independent. That is, most observational and experimental techniques have been designed with a particular species in mind. One of a handful of exceptions is the habituation-dishabituation paradigm, used to quantify an individual's ability to discriminate between two stimuli (see chapter 3). Thus developmental

psycholinguists (e.g., Eimas et al. 1971) have used this paradigm in studies designed to assess the human newborn's ability to make fine-grained phonemic distinctions, as well as its knowledge of the physical world (Baillargeon 1994; Spelke 1991, 1994). Recently, ornithologists have used this technique to look at the problem of categorical perception (Nelson and Marler 1989), whereas primatologists (Cheney and Seyfarth 1988) have used it to decode the meaning of vocalizations. Throughout the book, I will point to techniques that have been employed with different species and whether they yield results that can be directly compared. I will also discuss techniques that have been restricted to a particular species, but might be usefully implemented by researchers studying other species.

Within the past few years, statistical tools for phylogenetic comparisons have increased in sophistication and have gradually invaded behavioral ecological studies. This change is due in part to the efforts of Paul Harvey and his colleagues (reviewed in Harvey and Pagel 1991). The infusion of phylogenetic considerations has at least three important implications for the study of behavior. First, phylogenetic analyses can help us discern when a trait evolved, in how many lineages, and how long it survived over evolutionary time. Second, documenting phylogenetic relationships allows one to avoid statistical comparisons among nonindependent taxonomic units. Thus, for example, in studies of the evolution of brain size, species within genera often cluster, and thus species should not be considered as independent points. In this case, it is more appropriate to analyze the data at the generic level. Finally, comparative analyses often shed light on correlated traits. Identifying correlated traits is important because regression analyses typically require one or more variables to be partialled out so that one can directly assess the independent effects of one variable on the other. In the brain size example, we speak of dolphins, chimpanzees, and humans as having large brains *relative* to their body weights. We do so because brain size and body weight are, generally, positively correlated. In research on the neural structures subserving song production, we find that species with large repertoires have relatively larger song nuclei than species with small repertoires (DeVoogd et al. 1993).¹⁴

The comparative method is not without problems. The problems are most acute when phylogenetic relationships are poorly documented (e.g., ambiguities in the evolutionary tree due to incomplete molecular or morphological data) and when variables or traits are coded dichotomously as *present* versus *absent*. The latter

14. A few words of caution here. Some (Konishi and Ball, personal communication, unpublished data) have argued that the volume of song nuclei is more directly related to song output—how often birds sing—rather than to repertoire size. I give this issue a more thorough treatment in chapter 4.

problem is most relevant to the issues discussed in this book. The simplest way to illustrate this point is by referring to the heated debates in animal-learning psychology over the question of animal intelligence. Briefly, a great deal of research carried out from 1950 to 1980 focused on the possibility of general learning rules and cognitive abilities. Opponents of this view (e.g., Macphail 1987a, 1987b) argued that because interspecific comparisons were often made on the basis of a single experiment, it was not possible to distinguish between differences in performance and differences in ability. In terms of understanding the evolution of intelligence, ability is the most relevant measure.

The presence-absence distinction is at the heart of most discussions of language evolution. Although there is nothing theoretically misguided about this distinction, it must be used with caution. This is particularly the case in comparative studies of communication, where the units of comparison commonly differ between species (see chapter 3) and knowledge of the communication system is typically asymmetric for the species being compared. For example, it is often stated that a fundamental difference between human language and nonhuman animal communication is that the former has access to an infinite set of meaningful utterances whereas the latter is more restricted. The difference in expressiveness lies in the fact that language makes use of the combinatorial power of syntax whereas other communicative forms lack syntax. Although this distinction is currently accurate, it is perhaps premature. Only a handful of studies (see chapters 2, 3, and 7) have even broached the possibility of a nonhuman animal form of syntactical structure (Hailman and Ficken 1987; Hailman, Ficken, and Ficken 1985, 1987; Robinson 1984). There are two (related?) reasons for this sparsity. First, the unit of analysis for most studies of nonhuman animal communication is *the call or the song*. Strings of calls and song sequences are certainly produced by animals, and often such strings are comprised of heterogeneous call units. However, quantitative analyses of call sequences require complex statistics and large sample sizes (see chapter 3 for a more detailed discussion). The latter are often lacking. Second, there can be no formal study of syntax without first studying call meaning.¹⁵ The study of meaning is only in its infancy with respect to

15. In discussing the structure of nonhuman animal communication, Peter Marler (1977) has suggested that we distinguish between two types of syntax, *phonological* and *lexical*. Phonological syntax requires the combination of two or more acoustically distinct signals to create a new signal, the meaning of which is unrelated to the meaning of the components, if any. For instance, the word *came* can be arranged to create the word *mace*. There is some evidence that nonhuman primates, such as the capuchin monkey (Robinson 1984), cotton-top tamarin (Cleveland and Snowdon 1981), and gibbon (Mitani and Marler 1989) may exhibit phonological syntax. Lexical syntax is analogous to what most

nonhuman animal signals (see chapter 7). Until these two problems have been remedied, the evolution of syntactical abilities will remain unclear.

The last point I would like to make in this section is in reference to the distinction between homology (C. B. G. Campbell 1988) and homoplasy (Hodos 1988). As highlighted previously, if two species with a common phyletic history exhibit structurally similar traits, then we call such traits homologous. In contrast, if two species lack a common phyletic history but exhibit structurally similar traits, then such traits are considered homoplasies. Homoplasies typically arise because even distantly related species will confront environmental problems with a limited set of adaptive solutions. The distinction is important and relevant to comparative studies of communication because different evolutionary forces can be responsible for generating homologous and homoplastic similarities. For example, as described in greater detail in chapter 5, songbirds tend to go through a phase of vocal development known as subsong. During this phase, the young bird produces long, structurally diverse song monologues. The compositions of these songs are, in general, quite different from those produced in adulthood and yet contain similar elements. Like songbirds, human infants also exhibit a phase of vocal development where long, structurally diverse monologues are produced and such monologues consist of speechlike elements. In humans, this phase has been called *babbling*. Researchers working on avian song development (Marler 1970a, 1984; Marler and Pickert 1984) have suggested that subsong is like babbling. In this case, babbling and subsong represent homoplasies because humans and birds do not share a common ancestor who babbled or had subsong. In contrast to birds, there is only suggestive evidence that nonhuman primates go through a babbling phase (Snowdon 1982, 1990). If further work strengthens the claim, then babbling in human and nonhuman primates would be considered homologous, since both primates are likely to have shared a common ancestor who babbled.

1.3 Outline of the Book

This book was conceived as a purely scholarly scientific piece aimed at experts in the neurosciences, evolutionary biology, cognitive-developmental psychology, linguistics, and anthropology. As I began to research the various topics to be covered and talk to colleagues about the issues to be discussed, I realized that

linguists consider to be syntax *sensu stricto* and occurs when the meaning of a compound signal, whether consisting of parts of a word or several words, derives from the meanings of its components. Thus far, there is no convincing evidence of lexical syntax in the animal kingdom.

several courses were groping for a text that discussed issues in comparative communication. Consequently, I have attempted to write a book that is aimed primarily at the expert while being useful to those wishing to pick out pieces of the book for undergraduate and graduate instruction. The latter has been addressed at two levels. First, for each major topic I work through a small set of cases that I believe provide elegant and comprehensive studies of a particular process. For instance, in discussing the neurobiology of communication, I review some of the exciting new developments emerging from studies of birds and frogs where the finely choreographed interplay between perception and production systems has been extensively documented. By focusing on a relatively small subset of studies, students can learn to appreciate "the best of" from a given research area and hopefully understand how a problem is solved in the best of all worlds. In general, the case studies exhibit a taxonomic bias toward vertebrates, and more specifically, anurans, birds, and primates. The reason for this bias is that by sticking with these groups it is possible to maintain a level of conceptual continuity throughout the book that would not be possible with several other equally interesting organisms such as insects, fish, and reptiles. The case studies also exhibit a modality bias, restricted to communication in the auditory and visual domains. As a result, some of the fascinating studies on olfactory communication in insects and electric communication in fishes fail to make a significant appearance in the book. Although some of these organisms undoubtedly provide a better illustration of a particular phenomenon, the restriction I have imposed allows for a richer comparison across levels of analysis. Second, key concepts and methodological issues are flagged by providing compact discussions within "boxes," such as Box 1.1, "The Statistical Theory of Information." In contrast to the main text, each box provides a more clearly defined set of operational definitions, description of methodological techniques, and references to important review or primary articles.

Chapter 2 provides a historical overview of some of the different approaches to studying the evolution of communication systems, including the evolution of language. As highlighted in some of the previous sections, I find the history of work in this area particularly important because there is a tendency for the new generation to either ignore or misinterpret the older generation of work and, in some situations at least, for previous work to block our path toward a strong comparative research program. Additionally, some of the views espoused have led to highly testable predictions, many of which remain to be explored. Chapter 3 provides a basic introduction to conceptual issues in the study of communication, including a general discussion of the ecology of communication, an analysis of

problems associated with the definition and classification of fundamental units of communication, and a preliminary peek at how Tinbergen's research program can be worked out. Chapters 4 to 7 place comparative communication into the structure of Tinbergen's four causal questions, with the following modifications and subdivisions. Under the problem of mechanistic explanations of communication, I have created two chapters, one on neurobiology (4) and one on psychology (7). In essence, the topic of mechanism is divided into relatively low- and high-level neural processes. For chapters 4, 5, and 6, I have organized the case studies into three socioecological contexts—mating, survival, and socialization—focusing on both auditory and visual signals and cues. My motivation for organizing the examples into these three contexts is so that questions of design can be evaluated in light of evolutionarily significant problems. Thus, under mating, I describe the neurobiological specializations underlying anuran perception of advertisement calls and then discuss how sensory mechanisms coevolve with production mechanisms, leading to significant effects on the fitness of males and females. Chapter 7 also focuses on auditory and visual communication systems, but rather than looking at the contexts of mating, survival, and socialization, I concentrate instead on more general theoretical problems such as categorical perception and deception. Though there is no explicit chapter on phylogeny, I have attempted to address this gap by adopting a phylogenetic perspective throughout the book and, wherever it is relevant, referring directly to known phylogenetic relationships and historical constraints.

As a warning to the reader, let me note that the three contexts I have selected for discussing the design features of a communication system overlap considerably, and for some systems it is difficult to select a particular context. Thus signals and cues used during dominance-related interactions are clearly involved in socialization, but also serve an important function in survival and, ultimately, reproduction. The problem of contextual overlap becomes all the more challenging in discussing human communication. For purposes of organizational clarity, therefore, I have decided to cover human language under the socialization heading. Throughout the book, however, I will consider the possibility that the structure and function of language were shaped by problems associated with mating and survival, something that Darwin (1871) certainly believed.

Chapter 4 examines the neurobiological mechanisms underlying the production and perception of communication systems, focusing in particular on auditory signals. At present, little is known about the neurobiology of visual signals and cues, with the exception of primate facial expressions and human sign language. Chapter 5 explores the ontogeny of communication, using observational and

experimental data to assess the relative contributions of genetic and experiential factors to the developmental process. Chapter 6 discusses current understanding of the function or adaptive significance of different communication systems, looking at the question of design in light of how the production and perception of signals and cues influence individual fitness. Chapter 7 concentrates on the psychological mechanisms guiding the production and perception of communicative signals and cues. Specifically, I discuss the importance of feature extraction during categorization of visual and auditory stimuli, the "amount" of affective and referential information conveyed, and the extent to which individuals voluntarily communicate honest as opposed to dishonest information. The final chapter summarizes the general issues raised in the book, synthesizes the patterns uncovered, and provides a few specific suggestions regarding future research in comparative communication.

Enough warm-up. To work!

2 The Evolution of Communication: Historical Overview

2.1 Introduction

This chapter provides a topographical road map to some of the most dominant theoretical perspectives on the evolution and design of communication systems. The historical perspective is important for at least two reasons. First, some of the most luminary scholars of our time have dedicated their mental powers to speculations about the evolution of communication, and the ideas that have emerged provide explicit predictions about the form and function of communication systems. Interestingly, many of these predictions remain untested. In this historical treatment, therefore, I hope to lay bare some of the reasons for such conceptual dormancy and, along the way, to inspire more empirical work. Second, to avoid endlessly reinventing the communicative wheel, I develop the different theoretical perspectives in some detail so that current findings can be placed in a relatively unambiguous relationship to their historical origins. I begin in section 2.2 with a discussion of how biologists, dating back to Charles Darwin, have thought about the general design of communication systems. These ideas are rich, for they attempt to account for the structure and function of communication in all taxonomic groups, using a unified theory. In sections 2.3 and 2.4, I discuss a cluster of theoretical perspectives with a more narrow taxonomic focus. Specifically, these two sections concentrate on how linguists and biologists have attempted to explain the evolution of human language as a species-specific form of communication. Although narrow taxonomic analyses are not uncommon in biology, and this observation certainly applies to analyses of communication, human language evolution has been singled out here because of the considerable amount of critical discussion and controversy it has generated relative to other species and their communication systems. Needless to say, no study of language evolution has ever ignored the possibility of evolutionary precursors, visible within extant species. However, a range of views exist with regard to the importance of precursors, as well as to what "counts" as one. These different perspectives are relevant because they can guide our thinking about the significant design features of language, and what they do for the individual.

Section 2.5 is an attempt to reconcile some of the conflicting perspectives by arguing that a theoretical summation or averaging of the different views comes closer to a complete explanation of how communication systems evolved than any particular account viewed in isolation. In essence, the historical path we will travel in this chapter will lead us to an exciting position: by uniting different perspectives and levels of explanation, we can develop a coherent, synthetic treatment of the evolution of communication that attempts to encompass all