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A large fraction of all human behavioral variation is not simply the result of different individual adaptive responses to local ecological contingencies. Instead, the variation is partially determined by socially transmitted information that we call "culture." Although this is true for other species as well, the degree to which human behavior is influenced by socially transmitted information is exceptional. Most important, while "culture" in other animals consists of socially transmitted techniques and technological traditions needed to achieve specific adaptive ends, human culture consists of two additional types of socially transmitted information that may be absent in nonhuman species. First, learned social regulations of individual behavior in human societies shift the associated fitness costs and benefits in ways that affect all behaviors, from feeding to mating strategies. Second, humans universally develop systems of symbolic reinforcement of those regulations and show elaborate forms of display to signal adherence to a specific rule system.

Despite this rather obvious contrast, for most of my career as an anthropologist and behavioral ecologist, I would have argued that differences between humans and nonhumans in the importance of social learning were simply a matter of degree, not of kind. The diverse arguments of my cultural anthropology colleagues against this view did not dent my commitment to this position for many years. During this time I was mainly researching economic behavior and life-history patterns and felt that models borrowed from evolutionary ecology were quite productive for explaining human patterns in these areas regardless of "cultural" affinities (indeed, the optimality modeling approach that I employed was entirely culture free). Of course, I was aware that human behavior included components of social transmission, and these might even produce occasional maladaptive anomalies, but I felt that the same was likely true

for other social animals. To my mind, humans showed no qualitatively "unique" patterns, and the theoretical and methodological contributions from the study of animal behavior were impressive.

Although I still believe that systematic biologically informed research into human behavior is highly productive, two things have changed my view on behavioral modeling so that I now believe that human culture should be considered in all explanations of intergroup behavioral variability in humans. First, I spent almost half of the past 30 years living with remote hunter-gatherers and also observing primates in the wild. Despite the obviously useful application of animal behavior models to understanding human patterns, it is difficult to deny that even "primitive" hunter-gatherer societies seem extraordinarily complex in comparison with social primates. Hunter-gatherers themselves, who are quite sophisticated in their knowledge of animal behavior (Blurton-Jones and Konner 1976), soundly reject the idea that animal and human behavior are determined by the same forces. For example, indigenous friends that I met in Amazonia were upset when they were told that scientists like me were using "animal behavior" models (their view of "sociobiology") to explain indigenous cultural patterns. The suggestion that there were strong continuities in human and animal behavior was obviously insulting to them, and I began to wonder why. Similar stories surfaced in other areas of the world. Mardu Australian Aborigines were reported to identify with animals but viewed them as beneath humans because they copulated incestuously and failed to adhere to laws of kinship. The Hiwi of Venezuela pointed out that it was offensive to suggest that humans were "just another animal" because "animals have no shame" (i.e., guilt associated with breaking social rules). In short, hunter-gatherers, despite their affinity with nature, seemed to universally reject the notion that humans and animals were part of some simple continuum. Instead (and contrary to popular romantic myths), hunter-gatherers that I have known for over thirty years clearly hold the view that humans are qualitatively different from animals.

Second, when I began researching material for a synthetic overview of modern hunter-gatherers, I became bothered by a recurrent problem. Although behavioral ecological models clearly had the potential to explain many interesting patterns in the hunter-gatherer ethnographic literature, it seemed to me that a statistical control procedure would be necessary to demonstrate that fact. Specifically, casual inspection of my growing comparative database suggested that the strongest predictor of almost any hunter-gatherer pattern, whether it be polygyny level, infanticide rates,

warfare, food taboos, postmarital residence patterns, child-rearing practices, puberty rituals, or body piercings, was "ethnolinguistic membership." Groups from the same language families were often remarkably similar in some dimensions and in improbable ways even when they lived in different ecologies and somewhat distant from each other (this is equally obvious when we examine migrant groups dispersed throughout the modern world today). Likewise, geographic proximity appeared to be a strong predictor of specific behaviors irrespective of habitat type. Entire world regions of hunter-gatherers (e.g., Australia, California) showed enough commonalities in behavioral patterns despite habitat, linguistic, or genetic differences that such geographic "clustering" would have to be statistically controlled before testing explicit "ecological models" of hunter-gatherer behavior. The apparent need for statistical control of linguistic family and geographic region in order to test the effects of ecology on behavior (cf. Borgerhoff Mulder 2001) led me to reconsider the role of culture in human behavior. I began to recognize that most of my colleagues who studied human behavior from an adaptive perspective (behavioral ecologists and evolutionary psychologists) had mainly avoided the issue of "culture."

The question whether animals have "culture" is a semantic argument at one level; the answer is easily yes or no depending on definitions. If culture is nothing more than socially learned behavioral variation, then some animals are surely cultural. But for evolutionary biologists, the real question is, do we gain or lose in our ability to explain the special properties of *Homo sapiens* by employing the same term for the social traditions observed in animals and humans (Byrne et al. 2004)? My concern is that the loose application of the term "culture" for all socially learned behavior may obscure our ability to understand the evolution of what appear to be very unique characteristics of *Homo sapiens*. If humans are indeed as exceptional as they appear to be, we must describe more accurately their special characteristics rather than eagerly lump them with other social vertebrates.

I believe that anthropologists who work on human culture and biologists (for convenience I refer to all scientists who work on animal behavior as "biologists" in this chapter) who work on nonhuman "culture" have adopted very different understandings of the word "culture." This may be primarily responsible for disagreements in which biologists insist that animals do have culture, but anthropologists do not accept that view. Of course, there is also room for a third view, which is most

intriguing. We may accept the more elaborate anthropological definition of culture but still argue that some animal species show characteristics that meet this definition.

I am aware that some very astute researchers believe that arguing over the definition of culture is a useless exercise. Although I sympathize with the need to avoid semantic haggling, I do think that a clear specification of unique human properties is the first step to explaining the origins and evolution of our uniqueness. This does not necessarily mean rigid adherence to a culture/no culture dichotomy, but it does mean attempting to identify the characteristics that produce human uniqueness. Therefore, I intend to outline specifically what traits I think must be observed in any species to claim that it has "culture" as it has been defined in humans for more than a century. Here I focus on behavioral patterns rather than cognitive mechanisms. For example, it may be the case that "true imitation" rather than "emulation," "social facilitation," or some other social learning mechanism is required to produce cumulative culture, but from an observational point of view the lack of cumulative cultural adaptation in nonhuman animals is one trait that clearly distinguishes them from humans. Likewise, it may be that "teaching" is required in order to allow the social transmission of divergent social norms, but the resultant lack of enforced social norms are what notably distinguishes animals from humans (see below).

### Culture versus Social Learning

Biologists often equate socially learned behavior and resultant "behavioral traditions" with "culture." When local groups of animals, especially primates, exhibit suites of different behaviors not obviously attributable to local ecology, the groups are commonly referred to as different "cultures" (e.g., Wrangham, McGrew et al. 1994; Boesch 1996a; McGrew 2004; Sapolsky 2006), and such labeling has even led to a new field, "cultural primatology." Biologists have been particularly enthralled with the social transmission of feeding techniques and technology, from the milk-bottle-opening titmice to sponge-using dolphins and tool-wielding great apes. Because these observations combine both tool use and social learning, they seem especially similar to popular notions of human culture. Despite the popularity of equating animal with human culture, however, there have long been dissenters to this view (e.g., Galef 1992; Tomasello 1994). I agree that we should be very cautious about assum-

ing that animal traditions based on some type of social learning are equivalent to human culture. "Culture" as it has been defined and used in anthropology for more than a century consists of behaviors far more complex than socially learned tool use or the social transmission of foraging techniques or rates of aggression.

In the paragraphs that follow I will define "culture" from an anthropological perspective informed by evolutionary thinking. I suggest that animal "culture" probably differs from human culture in ways that have profound implications. First, socially learned information does not accumulate significantly in any nonhuman species (the so-called ratchet effect; Tomasello 1999a). Social learning allows human *populations* to successively modify and accumulate adaptive information over many generations, leading to the cumulative cultural evolution of adaptive techniques, technologies, and social institutions. Second, however, even if animals did accumulate socially learned technologies, they still would not be "cultural" in the human sense because critical components of the human culture complex are absent. Indeed, we may eventually find evidence of hominin species that show cumulative socially transmitted adaptations but are still not fully "cultural" in the same sense as modern humans. Specifically, the content of what is culturally transmitted may be unique in humans. The critical and unique components of "culture" are sufficient for humans to display unique behavioral patterns among living organisms, and they probably explain why both cultural anthropologists and Australian Aborigines set humans apart from all other species.

The earliest clear definition of "culture," provided by the founder of cultural anthropology, E. B. Tylor (1871, p. 1), is still the most widely cited: "That complex whole which includes knowledge, belief, art, law, morals, custom, and any other capabilities and habits acquired by man as a member of society." This definition does not simply equate social learning and behavioral traditions with "culture" but specifies types of socially learned information that compose the culture complex. Despite the fact that scholars had recognized since Aristotle (see Galef and Heyes 2004a, p. 1) that animals engaged in socially learned behavior, Tylor clearly felt that the label "culture" applied only to humans. Although I think that Tylor's insight was important, I also believe that modern evolutionary behavioral biologists can do even better. Tylor's definition has two weaknesses. First, it applies only to humans *by definition* and thus does not allow us to consider whether animals have "culture." Second, it includes behavior (i.e., "habits") as part of culture. As Cronk (1999)

noted emphatically, anthropological definitions of culture cannot include behavior as a component of culture if culture is then invoked to explain behavior. It is obviously circular to propose that behavioral differences (a component of culture) can “explain” behavioral differences (behavior). Biologists are also sometimes careless when they write about culture and behavior. To (unfairly) pick on one of the editors of this volume, Laland and Janik (2006, p. 542) defined culture as “all group-typical *behavior patterns*, shared by members of animal communities, that are to some degree reliant on socially learned and transmitted information.” They followed by suggesting that alternative explanations for behavioral differences in animals must include “consideration of the interplay between genes, ecology, and *culture*.” But, behavior cannot determine behavior. If culture is supposed to influence behavior along with genes and environment, we must then have a definition of culture that excludes behavior, and we must consistently use the term “culture” to refer only to nonbehavioral traits. I believe that most social scientists would probably be comfortable with a simple definition of culture such as: a historically derived set of shared ideas, values, norms, and beliefs that underlie behavior. Cultural “products” would then include behaviors and objects.

Despite some weaknesses in Tylor’s early definition of culture, he pointed out (as have most anthropologists) that culture consists of more than one informational component—it is a complex. Human “culture” is more than just socially learned tool use or food-getting “habits.” Tylor proposed that “culture” is a “complex” of traits that includes regulations on individual behavior (“law”) and the development of symbolic reinforcement apparatuses for that regulation (“religion and morals”).

Since Tylor’s time dozens of definitions of “culture” have been proposed, and anthropologists have never settled on a single definition. For example, Cronk (1999, Table 1) cites 20 different definitions of culture drawn from currently employed introductory anthropology texts. A handful of these must be rejected because they proclaim that “culture” is human by definition (e.g., Ferraro et al. 1994, p. 18) or too easily admit nonhuman animals to the culture club: “The capacity to use tools and symbols” (Bohannon 1992, p. 320). But the definitions that I believe are most useful to evolutionary biologists stress the complete set of informational components mentioned by Tylor. For example, Crapo (1996, p. 17) defines culture as “a learned system of beliefs, feelings, and rules for living around which a group of people organizes their lives.” Scupin (1992, p. 414) declares that culture is “a shared way of life that includes

material products, values, beliefs, and norms, that are transmitted within a particular society." Haviland (1996, p. 32) defines culture as "a set of rules or standards shared by members of a society, which when acted upon by the members produce behavior that falls within a range of variation the members consider proper and acceptable." These definitions all emphasize behavioral regulation and its symbolic reinforcement as critical components of culture.

Some evolutionary anthropologists have provided definitions of culture that may be too general. For example, Boyd and Richerson (1985) and Cronk (1999) propose that culture is "socially transmitted information." By this definition animals clearly have culture, but we must ask if there are some classes of information that are socially transmitted only by humans and whether or not it matters. If animals have culture too, why do they not form imaginary social boundaries around arbitrary groups of individuals that fight thousand-year wars and recruit suicide bombers to kill "infidels" who advocate a different lifestyle to be imposed on all? Perhaps in order to understand unique human traits we need to recognize the specific types of socially transmitted information that are a universal part of human culture but absent from nonhumans.

### Human Culture

I believe that human culture can be distilled to three critical components. Since culture is information, these are three categories of information that are socially transmitted. These components are universally found in all human societies. Many vertebrates show the first component, but no species that I am aware of has been reported to socially transmit the second and third components. This, along with the apparently unique human ability to generate extensive cumulative cultural change distinguishes humans from all nonhuman species.

The three universal components of human culture are the following:

1. *Socially learned techniques, technology, and environmental information (traditions, beliefs).* This component of culture consists of socially learned information about techniques and technology, as well as facts of nature and causal understandings of phenomena in the world. Because the information learned may be correct or incorrect, most scholars refer to these bits of information as "beliefs." Ways of doing things (traditions) and understandings of the world (beliefs) are passed along through

a variety of social transmission mechanisms but ultimately must be adopted by each individual that displays them. Although the transmission mechanisms evolve by natural selection and thus must increase fitness on average, these mechanisms will inevitably produce some maladaptive behaviors (Boyd and Richerson 1985).

2. *Regulations of individual behavior enforced by rewards and punishments (norms, conventions, institutions, laws).* These regulations set up the rules for the competitive game of life and constrain how resources and mates can be acquired. In evolutionary terms, norms change the fitness costs and benefits associated with behavioral alternatives. In human societies norms are institutionalized and apply to members of one abstract social category specifying the sanctioned rights and responsibilities toward members of other abstract social categories. This component of culture can frequently result in behaviors not predicted by acultural models. The different rules of any cultural group may arise spontaneously through response and counterresponse, or through some overt social bargaining process (this means that norms can be imposed to serve only the interests of a small group). Social rules of behavior are often explicitly developed to solve potential intragroup conflicts in the most efficient way and to facilitate group-beneficial cooperation in the face of public goods problems. Because many cultural rules encourage individual altruistic behavior that serves the common good and are backed by social punishment, this area of culture is closely tied to topics of “altruistic punishment,” “prosociality,” and “strong reciprocity” (Bowles and Gintis 1998, 2004; Gintis 2000; Fehr et al. 2002; Henrich and Henrich 2006). Strong reciprocators show “a propensity to reward those who have behaved cooperatively and correspondingly to punish those who have violated norms of acceptable behavior, even when reward and punishment cannot be justified in terms of self-regarding, outcome-oriented preferences” (Bowles and Gintis 1998, p. 1416). A defining feature of “strong reciprocity” is altruistic punishment: the willingness of individuals to punish noncooperators at a cost to themselves, even when the cooperative act cannot benefit them (or kin) directly (e.g., Fehr and Gächter 2002; Boyd et al. 2003; Fehr and Fischbacher 2004b).

Cultural rules are most likely to develop in order to regulate behaviors that can powerfully affect the fitness of a large number of group members. For example, among Ache hunter-gatherers there are strong cultural rules about cooperation during hunting and redistribution of the



kill after a successful hunt (Kaplan and Hill 1985; Hill 2002). Those rules have tremendous potential impact on both overall group food production and the daily share that is received by each individual in the social group. Indeed, the most common cultural rules in hunter-gatherer societies are about dividing up "resources," such as potential mates (marriage rules), acquired food resources (sharing rules), and access to food resources (territoriality), and about regulating conflict (rules for ritual combat, warfare, and settling disputes).

3. *Symbolic means of reinforcing, and signaling adherence to, a specific rule system.* The third component of human culture is a system of signaling in the form of rituals and ethnic markers, which exists in conjunction with the preceding rules component. Cultural signaling sessions are public and emotionally charged, using nonverbal channels in a highly effective fashion to reinforce the regulatory status quo (ritual) and often implying that the norms are linked to supernatural rewards and punishments (religion) in addition to reinforcement by a large majority of peers. They are designed to produce an emotional investment in the continuation of the rules (morality). Enforced rules are internalized to form values when individual actors deduce that a specific rule system serves their interests. Developing juveniles and adults gradually become committed to their own rule system because they have a comparative advantage under that system. The elderly are expected to be most conservative because they become experts at playing the game of life according to a particular set of rules that are often complex and difficult to master and they would be at a disadvantage playing under a new set of rules. They learn the effective ways to bend the rules to their advantage, as well as to impose them on others in ways that favor their interests. Because "rule abiders" generally prefer to interact with others who play by the same set of rules, signaling adherence in the form of adornments, dialects, ritual participation, and other behaviors (ethnicity) emerges as a means to obtain social partners, allies, and mates (cf. Boyd and Richerson 1987; McElreath et al. 2003).

The general idea that human culture consists of these three components has been recognized for more than half a century. For example, A. R. Radcliffe-Browne's (1922) ethnography of the Andaman Islanders is divided into three sections corresponding to the three components of culture: (1) utilitarian customs; (2) moral customs; (3) ceremonial customs. To date there is no animal "ethnography" that describes a complex of these three components for any nonhuman species.

## Animal “Culture”

Animal behavioral variants produced by social learning appear to be limited to two types of traits:

1. Locally common socially learned techniques and technology, behavioral tendencies (e.g., preferred mate choice, preferred foraging patterns, predator-avoidance tactics, and typical levels of aggression), and information about the world (tradition). These correspond to the first component of human culture but there is no evidence of cultural evolution or complex cultural adaptation that cannot be invented in a single generation through individual learning.

2. Socially learned symbolic mating and territorial songs and dances and the like (display). These mark territorial “in-group” membership, species membership, or alliance membership, but they do not appear to signal adherence to any socially enforced system of behavioral regulations. Whether these displays are conceptually similar to human ritual and ethnicity is something that must be carefully examined. Some of these traits (e.g., birdsong) do appear to change systematically through time, leading to new variants that are then socially transmitted to subsequent generations. This can lead to increasing signaling complexity in a few cases such as the coordinated choral structure of local groups of plain-tailed wrens (Mann et al. 2006), but this ability has not translated into more complex cooperative behavior (seen in all human societies) that allows for the utilization of new habits, resources, elimination of competitor species, and so on.

Most commonly reported examples of socially learned traditions in animals concern feeding techniques and technology, social interaction such as grooming, and greeting patterns and territorial or mating displays. Any recent review of the social animal learning literature (e.g., this book) contains dozens of examples of these in a wide range of vertebrates. Less commonly reported but equally important are socially learned mate-choice preferences (e.g., Galef and White 2000; Witte and Noltemeir 2002), aggression patterns (e.g., Sapolsky 2006), and the social transmission of predator-avoidance behavior (e.g., Griffin 2004). There is no doubt that over time the list of specific socially learned behaviors observed in nature will grow quite large and include categories as diverse as niche exploitation, nest-building techniques, and parenting behavior. When all these are considered, however, only the observation of social traditions in greeting and mating or territorial displays fall outside the

first component of human culture. But unlike the human cultural signals, these social displays do not signal adherence to a rule system in order to attract partners who adhere to the same set of behavioral regulations. Likewise, there are no animal rituals designed to reinforce a social rule system or elicit emotional commitment to a particular rule system (morality). Thus critical components of human culture appear to be lacking even in our closest phylogenetic relatives. For example, none of the 39 culturally variant traits reported in Whiten et al.'s (1999) article on chimpanzee "culture" is a clear example of the second or third components of human culture, but a similar study of regionally independent human populations would show hundreds of examples of cultural variation in these components. In short, animals show socially learned traditions, but there is no evidence in any animal for socially learned conventions, ethics, rituals, religion, or morality, which are critical and universal components of human culture.

### Examples of Hunter-Gatherer Cultural Regulations

I have suggested that animal social traditions do not constitute culture as defined by anthropologists because animals do not engage in socially learned regulation of behavior enforced by third-party punishment and reward. Although modern societies and large-scale state societies throughout history have developed an almost infinite number of formalized behavioral regulations codified in written laws, even the simplest hunter-gatherer societies illustrate this universal human pattern. Hunter-gatherers universally regulate access to valuable resources (e.g., food, mates) and regulate how competition for these resources may be legitimately expressed. And hunter-gatherers sometimes formally specify punishments or payments imposed on those who violate the norms. Here are some examples of the most common regulations reported in hunter-gatherer ethnographies, and many societies show nearly all the regulations mentioned on this list.

### Social Norms Regulating Behavior

1. Mate access
  - a. Prohibitions and prescriptions (applied on the basis of age, kin, or ritual-group membership)
  - b. Polygyny (degree allowed and who may practice it)

2. Food production
  - a. Land use (territoriality)
  - b. Specific resource rights (ownership of specific plants or animals)
  - c. Niche specialization (informal trade unions)
3. Food redistribution
  - a. Sharing (who receives, how much they receive, and, what body parts of some game species)
  - b. Consumption taboos (applied on the basis of age, kin, or ritual-group membership).
4. Display rights (ritual participation)
  - a. Mating (who may participate in organized displays that are important forums for mate choice)
  - b. Other sociopolitical messages (who has the right to “broadcast” symbolic messages and in what context)
5. Access to kin and other allies
  - a. Residence rules (who is allowed to reside with close kin)
  - b. Activity and ritual regulations (who can be a member in some organized activities)
6. Political power
  - a. Designated positions (reserved for specified age, sex, kin or ritual-group members).
  - b. Transfer of power (rules of succession, turn taking, or context-specific leadership)
7. Regulation of violent conflict
  - a. Within-group contests (ritual dueling, divining, and justice)
  - b. Participation in social group defense (who may or must defend the group and in what contexts)
8. Regulation of life history
  - a. Age at first reproduction (acceptable age for sexual relations and marriage)
  - b. Investment in infants and juveniles (who must invest and in what contexts)
  - c. Age- and sex-specific rights and restrictions (that change during the life course) in competition over resources

## Human-Specific Psychological Mechanisms of Culture

Because human and animal culture contain different components, we might expect that different psychological mechanisms underlie them. The first component of culture, socially learned techniques, technology, and information, is produced through at least half a dozen different learning and imitation mechanisms, only some of which may be distinct in animals and humans (e.g., Tomasello 1999a; Whiten et al. 2004; Byrne 2005). However, the second and third components of human culture, norms and their symbolic reinforcement, may emerge through additional processes including teaching, strong conformity bias, and cognitive mechanisms that add value judgments to the behavior of third parties. Cultural regulatory systems are backed by strong emotional responses to those who break them. Thus, when norms are transmitted, juveniles both accurately imitate the actions of adults, and also incorporate a moral sense that to do things otherwise is "wrong" (Tomasello, this volume). Humans experience feelings of anger, fairness, justice, indignation, guilt, and so on and categorize other humans as "jerks," "assholes," "self-centered," "egotists," "sleazeballs," "criminals," "villains," and so on when they violate social regulations. Individuals in different societies react to different behaviors (e.g., copulating with a clan member or an underaged partner, eating a taboo food, or speaking to a parent-in-law) as "disgusting," "revolting," "repulsive," "vile," "abhorrent," "deranged," and so on. There is little evidence that primates show similar emotional responses to deviants who fail to adhere to the local socially learned traditions.

Human social regulation of cooperation and competition has led to the codification of personal and property crimes and the recognition that some individuals are "victimized" by those who fail to adhere to social norms. Additionally, for humans, some "crimes" have no obvious victims (e.g., prostitution, drug use, consensual homosexuality), but still induce an emotional reaction and are punished by observers, most likely because people are invested in the rules themselves and in a belief that they can compete most successfully if certain behaviors are disallowed.

When a baboon is attacked by another larger baboon, it may feel fear and think about how to escape. Humans, in addition, categorize events of conflict (but not with computers or other animals) as "justified" or "unjustified" and have a strong emotional response to the latter. For

example, experiments have shown that people experience a strong emotional reaction when human partners in the ultimatum game make “unfair” offers (highly unequal division of the original stake that favor the divider), but they do not show the same response to a computer that makes the same division (Sanfey et al. 2003). Instead, they simply accept the skewed offer if it will maximize their monetary gain. Chimpanzees seem to react the same way when playing each other in the ultimatum game (Jensen et al. 2007).

Humans, on the other hand, appear to have evolved an emotional mechanism to promote cultural behavior that we refer to as “conscience.” Conscience is revealed in behavior as a concern for the welfare of others, or an “other-regarding preference” (Fehr and Fischbacher 2003). To date, it appears that most animals, including chimpanzees (Silk et al. 2005; Vonk et al. 2007), do not show prosocial tendencies but are instead “sociopaths/psychopaths.” Hare (2006, p. 58) describes psychopaths as “intraspecies predators who use charm, manipulation, intimidation, and violence to control others and to satisfy their own selfish needs. Lacking in conscience and in feelings for others, they cold-bloodedly take what they want and do as they please, *violating social norms* and expectations without the slightest sense of guilt or regret.” Such behavior, while perhaps typical in most animals, is considered pathological in humans and is estimated to be expressed by only about 1 to 4 percent of the population (Pitchford 2001; Stout 2005). Psychopaths show no remorse, empathy, anxiety, or guilt. These may be the emotional adaptations most associated with human culture and strong reciprocity, as well as the features of human cognition that are more important than imitation mechanisms for distinguishing human from animal culture.

Researchers have long recognized that there is a potential adaptive niche for sociopaths even in human societies that punish such behavior (Harpending and Sobus 1987; Mealey 1995). The continued prevalence of purely self-regarding rule breakers in all human societies probably indicates that alleles producing emotional indifference to norms exist over extensive time periods in a balanced ESS with more cooperative norm-abiding alleles (Bowles and Gintis 2004). Indeed, recent studies also suggest that a minority of humans show no tendency to engage in reciprocity/cooperation (Fischbacher et al. 2001; Kurzban and Houser 2005). But purely self-regarding individuals can be induced to behave as cooperators if they believe that the majority of other individuals in their society are strong reciprocators (Camerer and Fehr 2006).

The deep feelings of guilt and anger over injustice are emotional responses that are expressed in all human societies. The universality of these traits implies that their origin took place before the last common ancestor of modern humans. The existence of strong automatic emotional responses to breaking agreed-on social norms indicates that punishment of those who cheat on social norms has been a component of human natural history long enough for the emotional mechanisms to evolve. But since we know little about the rate of evolution for such mechanisms, we must rely on other evidence to ascertain when cooperative social norms first emerged.

### Even Neanderthals May Not Have Had "Culture"

Despite the fact that some biologists propose "culture" as a characteristic of numerous social vertebrates, I think it quite possible that complete "culture" as defined by anthropologists is very recent and unique to *Homo sapiens*. Some hominins may have evolved social learning mechanisms that produced cumulative cultural adaptations early on. Achuelian tools may be early signs of this (depending on whether hand axes were the goal or by-products of tool making), as is perhaps the ability to live at far northern latitudes by 1.7 million years ago (Vekua et al 2002; Zhu et al 2004). Throwing spears by 400,000 years ago (Thieme 1997) seem too complex to explain without progressive cultural adaptation, and the Mousterian tool kits used by Neanderthals indicate cumulative improvement on earlier technological traditions that culminates in improbable complexity—composite tools and hafting (d'Errico 2003). But none of these provides evidence for enforced social norms or the signaling that promotes them.

While direct evidence of social norms might be difficult to obtain, the ethnic signaling of adherence to a specific set of norms is more perceptible in the archeological record. Based on that evidence, complete "culture" including social norms and ritual and ethnic signaling, may have existed only for the past 160,000 years or so (Henshilwood and Marean 2002; Marean et al 2007; McBrearty and Stringer 2007) and only in *Homo sapiens*. However, the earliest date of ethnic marking is difficult to ascertain because the earliest evidence of symbolic display comes in the form of pigment use, something that may represent extrasomatic mating display of phenotypic quality (similar to bower birds) rather than ethnic marking.

Whether or not Neanderthals maintained social norms and ethnic marking is unclear. Many anthropologists have noted apparent cognitive differences between modern humans and Neanderthals. Wynn and Coolidge (2004, p. 468) note that Neanderthal technology is functionally as advanced as that of early humans, and hunting and gathering techniques were similar. "But . . . Neanderthals never fully acquired the trappings of modern human culture . . . Such a pattern of coexistence for millennia without acculturation does not fit easily into anthropology's understanding of culture process." "It appears necessary to posit a cognitive/neurological difference between Neanderthals and modern humans." Indeed, the lack of Neanderthal acculturation to human patterns (presuming likely exposure) is reminiscent of the chimpanzee ability to faithfully transmit food-getting techniques along a chain of social transmission within and between groups (Horner et al 2006; Whiten et al 2005) but the inability of chimpanzees to socially acquire a more efficient food-getting technique when exposed to a new model after they have already learned a less efficient one (Marshall-Pescini and Whiten in press). In any case, Neanderthals show only minor evidence of norms, ritual, and ethnicity, and the observed Neanderthal traditions might best be labeled "protocultural." After detailed examination of early modern human grave goods, Wynn and Coolidge (2004, p. 480) conclude that "such burials stand in stark contrast to Neanderthal burials, where there are few, if any, convincing examples of grave goods." Evidence for Neanderthal art is ambiguous or lacking, although they may have used ochre or mineral pigments (d'Errico 2003), but again this is possibly extrasomatic mating display rather than ethnic signaling. If Neanderthals did develop simple social norms and practice incipient ethnic signaling, this does not seem to have led to extensive cooperation and between-group competitive advantage that produced spectacular cumulative cultural evolution as is typical in humans (Soltis, Boyd, and Richerson 1995; Boyd and Richerson 2002; Henrich 2004b). This lack might possibly explain the replacement of Neanderthals by *Homo sapiens* (Hill et al in press).

Whether Neanderthals possessed the evolved emotional underpinnings of cooperative morality is also difficult to assess. As Tattersall (2002, p. 129) points out, "We have no idea what the Neanderthals were like temperamentally: whether they were aggressive or retiring; cooperative or individualistic; forthright or sneaky; trusting or suspicious; crude or lovable; or like our own species, all of the above." Although Neanderthals



were heavily dependent on game and probably shared their kill with social group members, so do many other species of social hunters, especially the cooperative breeder species. But did Neanderthals develop extensive cooperation between nonkin through enforced social regulations and did they evolve the accompanying emotional mechanisms associated with norm enforcement? If so, there is little archeological evidence that they engaged in norm-promoting rituals and symbolic ethnic marking found in all societies of *Homo sapiens*.

### Conclusion

Animal "traditions" appear to differ from human "culture" in two ways (cf. Whiten, this volume). First, there is no significant accumulation of information through social learning in nonhuman animals, leading to cultural products of ever more increasingly adaptive complexity. Although some animals have shown rudimentary cultural accumulation (e.g., crows: Hunt and Gray 2003; macaques, as described in McGrew 2004, p. 23), the difference between animals and humans is likely to be rooted in some deep cognitive differences. Humans alone appear to have a strong innate taste for engaging in unrewarded imitation, especially in childhood (but see McGregor et al. 2006) and an orientation toward "shared intentionality," helping, conformity, and attaching moral judgments to others who are unwilling to conform (Werneken and Tomasello 2006; Tomasello, this volume). Finally, human cognitive mechanisms that produce modifications (often much later in the lifespan) of previously copied behaviors may differ in ways that lead to a greatly expanded tendency to innovate the methods that can serve as models for the next generation of social learning.

Second, there are important content differences in cultural traits. Animals do not engage in social transmission of certain types of information that result in the social regulation of behavior, or in symbolic reinforcement of particular systems of rules and institutions that regulate behavior. Animal species that exhibit local traditions but do not have moral systems and do not reinforce social rules with symbolic display or signal adherence to specific sets of norms do not have "culture" as it has been defined by anthropologists. Local behavioral variants of nonhuman species should thus be referred to as "traditions," not "culture."

In order to employ the term "culture" consistent with traditional usage and without the term carrying a separate meaning for humans and

for other animals, biologists must provide empirical evidence that is still lacking. For example, chimpanzees engage in meat sharing, and it is patterned, but for this to be “cultural,” there must be observations of altruistic third-party punishment imposed on individuals who break meat-sharing conventions. Otherwise sharing patterns may simply represent a combination of self-interested foraging, reciprocity, unacceptable costs of resource defense, and costly signaling, all determined by the size and timing of prey acquisition by coresident group members (e.g., Gurven 2004). Finally, chimpanzee meat sharing would not be considered fully “cultural,” in the anthropological sense unless chimpanzees engaged in symbolic display to signal which meat-sharing norm they adhere to, and engaged in symbolic activities designed to encourage group members to continue practicing the same norm in the future. If chimpanzees did regularly develop alternative socially transmitted sets of norms about meat sharing, described above, we might also expect evolved emotional responses of injustice, indignation, or anger upon observing another chimpanzee breaking those rules, (even when the observers were not directly affected). This, I believe would indeed make chimpanzees “cultural.” (It would probably also qualify them as “human” for purposes of human-chimpanzee interaction—a goal that has long eluded animal rights activists.)

The view I present implies that “culture” has a moral component. I am aware of occasional reports of possible primate morality (e.g., de Waal 1996a), but retribution against defection in reciprocity is not equivalent to evidence of “morality.” Selfishly amoral individuals are expected to reciprocate if it increases the likelihood of future fitness gains, and to object to defection against them. Thus, contingent reciprocity in some primates (e.g., Hauser et al. 2003) does not demonstrate commitment to a set of “moral” principles. Even observations such as the reported rejection of unequal rewards in capuchin monkeys (Brosnan and de Waal 2003) does not indicate the willingness to pay a cost to uphold a set of values (cf. Henrich 2004a). Only if primatologists report observations of nonkin altruistic punishment of norm violations will the proposal of primate morality be convincing. Morality is demonstrated by altruistic third-party punishment. To my knowledge the only potential examples of this come from specialized cooperative breeders and maybe eusocial insects where individuals who do not contribute to raising offspring are often punished, and possibly by individuals unrelated to the juveniles being raised (Clutton Brock 2006).

Culture is the apparent hallmark of human uniqueness, and whether any other species shares this trait, even in rudimentary form, is an extremely important evolutionary question. As scientists, accounting for exceptional human adaptability is one of our most exciting challenges. Culture is an obvious candidate for human uniqueness, but explanatory models that focus only on traditions and transmission mechanisms may not bring us the full understanding we seek. A focus on the unique qualities of transmitted information in human societies may also be critical. The study of complex adaptive behavioral rule systems, how they emerge, how they change, how they spread, how they are stabilized, and how they are enforced, will probably bring us closer to understanding the human-animal gap than the study of cultural techniques and technologies. A chimpanzee that can make a spear is still not human. Perhaps my hunter-gatherer friends are correct in their belief that humans are not just another animal. It would take some very rigorous science and a number of new observations to show that this commonsense view is incorrect.