

What Cultural Primatology Can Tell Anthropologists about the Evolution of Culture

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Abstract

This review traces the development of the field of cultural primatology from its origins in Japan in the 1950s to the present. The field has experienced a number of theoretical and methodological influences from diverse fields, including comparative experimental psychology, Freudian psychoanalysis, behavioral ecology, cultural anthropology, and gene-culture coevolution theory. Our understanding of cultural dynamics and the evolution of culture cannot be complete without comparative studies of (*a*) how socioecological variables affect cultural transmission dynamics, (*b*) the proximate mechanisms by which social learning is achieved, (*c*) developmental studies of the role of social influence in acquiring behavioral traits, and (*d*) the fitness consequences of engaging in social learning.

INTRODUCTION

The study of culture has been central in the field of anthropology since the founding of the discipline. The question of how the human cultural capacity evolved is one of the few questions to which all four subfields of anthropology can make significant and complementary contributions. The purpose of this review is to describe the progress that cultural primatology has made in defining how cultural processes operate and how culture evolved, and to relate this progress to research efforts in other branches of anthropology.

One of the problems that has hampered anthropology's progress as a cohesive discipline in studying culture is the lack of a commonly shared definition of what culture is. There are hundreds of definitions, but most fall into two classes: those focusing on observable behavioral variation, and those focusing on the mental processes or constructs responsible for producing cultural variants. Because of the difficulty in directly accessing the contents of nonhuman primates' minds, cultural primatologists have adopted the former type of definition. Here I define culture as behavioral variation that owes its existence at least in part to social learning processes, social learning being defined as changes in behavior that result from attending to the behavior or behavioral products of another individual. This definition of culture will be viewed as overly simplified by some scholars, but it has the advantage of being easily operationalized and relevant to both humans and nonhumans. Also, it captures the core element of all previous definitions in cultural primatology and virtually all previous definitions within cultural anthropology: the idea that information, skills, practices, or beliefs are transmitted via social inheritance rather than through genetic inheritance [see Laland & Hoppitt (2003), Durham (1991), and Kroeber & Kluckhohn (1952) for further discussion of definitions of culture].

CULTURAL PRIMATOLOGY: HISTORY OF APPROACHES

Japanese Foundations

The field of cultural primatology was founded by the Japanese researcher Kinji Imanishi, who in his 1952 paper on "The Evolution of Human Nature" inspired Japanese primatologists to search for between-group differences in behavior in nonhuman primates. In the decades that followed, a group of dedicated researchers produced a steady stream of papers documenting interesting within- and between-site variability in the diet, food-processing techniques, courtship signals, bathing habits, grooming techniques, and solitary play habits of Japanese macaques, *Macaca fuscata* (reviewed in Itani & Nishimura 1973, McGrew 1998, Perry & Manson 2003). These papers are noteworthy for their richness of description of the transmission process; many report the precise order in which individuals acquired novel traits and discuss this finding in the context of the social organization of the group, reporting group members' kinship, rank, and spatial organization. In these early papers, researchers assumed that behavior was determined either by species-universal "instinct" or by "culture," i.e., that variability in behavior was necessarily a consequence of culture. They did not seriously consider the possibility that subtle variations in ecology or individual experience could induce individuals to behave differently from conspecifics at other places owing to asocial learning processes.

"Cultural Panthropology" and its Offshoots

With rare exceptions (e.g., Green 1975, Stephenson 1973, McGrew & Tutin 1978, Hannah & McGrew 1987), Western scientists ignored the developing field of cultural primatology until the 1990s, when the community of chimpanzee (*Pan troglodytes*) field researchers began reporting striking intersite

behavioral variation, particularly with regard to tool use (e.g., Boesch 1996, Nishida 1987). This body of research received far more attention from the scientific community generally, in part because more of it was written in English and in part perhaps because anthropologists found it more plausible to accept the notion of culture in the closest living relative to humans than they did in a monkey species. The goal of many of these early chimp culture papers was apparently to convince cultural anthropologists that humans are not alone in exhibiting culture, that there is evolutionary continuity between humans and other primates regarding cultural diversity and reliance on social learning. These publications (particularly Boesch 1996, McGrew 1992, Whiten et al. 1999) focused on documenting the geographic distribution of behavioral variants across study sites, creating a sort of "chimpanzee relations area file." One strength of this body of work is the acknowledgment that not all between-site behavioral variation is necessarily cultural in origin; some variation may be due to intersite genetic variation or to ecological differences that lead individuals at different sites to arrive at different behavior patterns because of asocial learning processes (i.e., trial-and-error learning) (Nishida 1987, Whiten et al. 1999). However, in contrast with the earlier Japanese macaque research, the chimpanzee field researchers rarely described in their "culture" papers the relevant aspects of within-community social dynamics that may have produced the observed patterns of behavioral variation. Perhaps in part for this reason, nonprimatologists reading these lists of putative cultural differences (divorced from descriptions of the complex social dynamics of chimpanzees that are presumably involved in creating and maintaining these variations) perceived chimpanzee "culture" as rather sterile in comparison with their conceptions of human culture. It is not entirely clear why the chimpanzee researchers abandoned the Japanese researchers' tradition of supplementing discussions of social transmission sequences with richly detailed "simian so-

ciology." Perhaps it is because transmission chains are harder to document accurately in a fission-fusion species like chimpanzees, in which all members of the same social group are rarely found in the same place at the same time, than in stable social groupings like those of macaques. Also, behavioral analyses that are relatively easy to accomplish for stable social groups can be methodologically more difficult in fission-fusion species, in which most group members are out of view of one another most of the time, and not all dyads have equal opportunities to interact with one another. Another factor may be that the two most prestigious scientific journals (*Science* and *Nature*) limit contributions to a few pages, making it impossible to report the contextual detail that was typical of early Japanese cultural primatology. Certainly the chimpanzee researchers writing about culture were well aware of the complexities of chimpanzee social structure and relationship negotiation; in fact, some of them had written extensively about these topics in other venues. They simply had not integrated this information into their articles on culture to the extent that Japanese researchers had.

The landmark publication of the "cultural panthropologists," to use Whiten's (2003) memorable phrase, appeared in *Nature* and included an impressive list of 39 behavior patterns (*a*) that were present in some chimpanzee communities but not others and (*b*) for which ecological explanations of the geographic variation seemed improbable (Whiten et al. 1999). This paper set chimpanzees apart from other nonhuman primates as the species having the most elaborate cultural diversity. However, similar collaborative studies had never been performed on other species; it is quite likely that the "behavioral diversity gap" between chimpanzees and other primates will shrink once equivalent studies are performed, just as the Whiten et al. (1999) study shrank the gap between chimpanzees and humans. One other study, on orangutans, of similar design has been published since Whiten's. Orangutans seem like

unlikely candidates for cultural diversity because they lead a more solitary existence than practically any other anthropoid primate, yet van Schaik and his colleagues (2003) documented 24 behavioral variants suspected to be cultural in a study comparing 6 study sites in Sumatra and Borneo. The orangutan's virtually solitary life makes it, in some ways, an ideal candidate for documenting the acquisition of behavioral traits from particular social partners because each individual has extensive contact with only one or two other associates. Thus, Russon (2003) has the best data set documenting social influence on development of foraging techniques for any wild ape, and her data make more plausible the claim that the intersite variation seen in orangutans is truly cultural in nature. Recent work by Whiten et al. (2005) on captive chimpanzees also lends credence to the idea that observed patterns of variation in the field are possibly socially learned by demonstrating that (*a*) individuals can acquire new techniques for gaining food by watching a group member who has been trained by an experimenter, and (*b*) chimpanzees who know multiple techniques tend to conform to the technique predominantly used by their companions.

Many theoretical reasons show that traditions are as common in many monkey species as they are in apes and that they simply have not been discovered owing to lack of research effort by researchers interested in such questions (Perry & Manson 2003). In general, monkeys live in social settings in which they have a larger number of social contacts from whom they could acquire behavioral practices, relative to those apes (chimps and orangutans) in which cultural diversity has been documented best. Also, many monkeys are omnivorous (which should make social cues useful in making food choice decisions) and engage in extractive foraging (which would make tool use and other complex foraging techniques useful). Likewise, many monkeys exhibit cooperative social relationships and live in complex social environments of the type that might necessitate extensive

communication about their relationships and promote the development of flexible bond-testing rituals (Perry et al. 2003a).

Mechanisms of Social Learning

While field researchers in the 1990s were busy documenting behavioral variations in chimpanzees, laboratory researchers were hard at work documenting the cognitive mechanisms underlying cultural transmission. Early work on the cognitive psychology of social learning was guided by two conflicting anthropomorphic assumptions, both of which turned out to be false to some degree. Because imitation (copying of a model's motor actions) comes so easily to human children, and because folklore about primates is riddled with "monkey see, monkey do" stories, some researchers (e.g., the early Japanese primatologists) started with the assumption that imitation must be easy, a cheap trick for learning many new skills quickly. Other researchers, noting that extreme cultural elaboration in humans greatly exceeded cultural capacities in nonhumans, assumed that some extremely complex cognitive machinery must be necessary to produce culture; therefore, they speculated that there would be sharp differences between humans and apes, and likewise between apes and monkeys, in their capacities to learn socially, innovate, and form traditions. Tomasello & Call (1997), in their review of the literature, found considerable evidence for simple forms of social learning such as local and stimulus enhancement (i.e., being attracted to a particular object or location with which a model is engaged) and emulation learning (observational learning of the cause-and-effect relationships created by a model's manipulations) in both monkeys and apes. The apes were better than monkeys at emulation, and human-raised apes were far better at imitation than either ape-reared apes or monkeys. The general conclusion by the early 1990s was that copying motor actions was easy for humans, difficult for apes (although present at least in human-reared, i.e., "enculturated," apes) and

essentially absent in monkeys (Byrne 1995, Tomasello 1996).

Some of the most detailed and careful work on social learning was performed on captive brown capuchin monkeys (*Cebus apella*) by Frigaszy's and Visalberghi's labs (see Frigaszy et al. 2004 for a review of this body of work). The tasks that they gave their animals were all centered around food choice and food-processing techniques (some requiring merely dexterity, such as foraging on pumpkin seeds, and others requiring tool use such as nut cracking, obtaining peanuts from inside glass tubes with sticks, and operating a juice dispenser). The general conclusions from these experiments were that social influence is important in the development of particular skills and preferences but that relatively simple social-learning processes such as social facilitation (an increase in a behavioral element already present in the repertoire that is contingent on concurrent performance of the same behavior by others in the vicinity), stimulus enhancement, and local enhancement, rather than imitation, are typically employed by the monkeys. For example, in the food choice experiments, the subject monkeys were stimulated to increase their consumption of both novel and familiar foods when the demonstrator monkey was also eating, but they did not prefer the particular food eaten by the demonstrator (Visalberghi & Addessi 2003). They argued that capuchins' tendencies to coordinate their activities in space and time channel their behavior such that they are likely, in the wild, to end up trying the foods eaten by the more knowledgeable members of their social group, even if they do not attend very well to the specific properties of those foods. Capuchins who were given ample opportunity to observe experienced monkeys poking sticks through tubes to remove the peanuts inside them failed to show that they understood the relevant aspects of the tube, implying that they were not imitating the model. Again, it seems that capuchin monkeys do gain an enthusiasm for particular tasks and objects by watching others engage in them, even though

they do not learn fine-grained details about the way in which objects are to be manipulated. Visalberghi (1993) and Frigaszy et al. (2004) concluded that the role of social influence is to channel the monkeys' attention toward particular objects and general activities, after which they gain knowledge of the task via trial-and-error learning.

Puzzlingly, however, results from wild *Cebus capucinus* in the field indicate that young capuchins do visually attend to the specific properties of foods being processed by groupmates: They show significant preferences for observing groupmates who are foraging on food items that are rarer in the diet, as well as those items that require more complex processing, which suggests that they are seeking out rather specific information about what to eat and how to process food (Perry & Ordóñez 2006). Data from wild *C. capucinus* also show that the more time pairs of monkeys spend in close association with one another, the more likely they are to share a particular foraging technique (Panger et al. 2002; S. Perry, unpublished observations); such results are difficult to reconcile with a social-learning model that excludes imitation entirely. Although imitation is difficult for most nonhuman primates, and it is not nearly so often employed in their daily lives as are the cognitively simpler social-learning mechanisms, imitation is nonetheless possible for many nonhuman primates under a narrow range of circumstances. This interpretation is consistent with one captive study that produced some suggestive evidence that capuchins can imitate under certain conditions, although they appear to do it quite rarely (Custance et al. 1999).

Numerous studies of imitation have been done in a variety of taxa in the past decade, and now the distinctions drawn previously are less well defined (see Whiten et al. 2004 for a review of social learning in apes). Researchers have documented imitative capacities not only in chimpanzees and orangutans, but even in callitrichids (Voelkl & Huber 2000) and in some nonprimates (e.g., birds: Zentall 2004).

To summarize the state of the literature on social-learning mechanisms, the picture is still murky as to which mechanisms are employed by which species and under which circumstances, and much work is still needed to sort out this mess (see for example Whiten et al. 2004). There are, however, some clear take-home messages. All primate species that have been thoroughly investigated rely on a number of social-learning mechanisms, some of them quite simple (e.g., attraction to locations occupied by groupmates or to objects being handled by groupmates) and others perhaps more cognitively challenging (such as association of an object with a particular behavioral goal; or imitation of fine motor details). The simpler mechanisms are more commonly employed than is true imitation in monkeys, apes, and even humans (Tomasello 1999). True imitation is not an exclusively human cognitive trick, but it is certainly more commonly used by humans than by other species (Boesch & Tomasello 1998, Tomasello 1999). One of the main challenges for psychologists working in this area will be to determine which factors trigger the use of certain types of social-learning mechanisms as opposed to others. Which features of the task, of the demonstrator, and of the social context stimulate the animal to pay attention to details such as the physical properties of the objects being manipulated (e.g., color, smell, size, shape), the motor movements of the demonstrator, the apparent behavioral goals of the demonstrator (as determined by the consequences of their actions), or the movements of manipulated objects relative to other objects?

Cultural Transmission Theory

The study of culture in nonhumans became far more interesting theoretically when behavioral ecologists began to focus on culture. Theoreticians such as Boyd & Richerson (1985), Cavalli-Sforza & Feldman (1981), and Laland (Laland & Kendal 2003) began to model gene-culture coevolution and to promote cultural transmission as a topic that had

relevance to biology (see Richerson & Boyd 2004 for an accessible account of the ideas expressed by these formal models, and Durham 1991 for empirical examples of gene-culture coevolution). For the first time, culture was viewed as a topic of serious scientific inquiry in biology, and behavioral biologists were captivated by the idea that certain behaviors could be inherited socially in a manner roughly analogous to the way in which genetic inheritance occurs. Laland and his colleagues (Laland & Kendal 2003, Odling-Smee et al. 2003) were particularly influential as ambassadors of gene-culture coevolution theory to primatologists, and they emphasized that socially learned behaviors could alter the environment in such a way that the modified environment exerted selective pressure on genetically inherited traits. This process by which animals can, by their own behavior, alter the selective pressures on future generations was dubbed niche construction (Odling-Smee et al. 2003). Although I know of only one empirical study in primatology that directly incorporates this idea (Flack et al. 2006), it was nonetheless an effective attention getter in that it branded social learning as a topic of evolutionary importance and thereby diverted research effort toward social learning in general.

The Socioecology of Animal Social Learning and Traditions: What, Why, When, and Who?

Once more behavioral ecologists joined the cultural primatology bandwagon, the research emphasis started to shift away from the question "Does Species X have culture?" to more theoretically interesting questions such as "Under which conditions should individuals engage in social learning?," "Who should an individual copy?," "How do various socioecological variables affect the dynamics of social transmission?," and "What adaptive benefits accrue to animals who engage in social learning?" (see Laland 2004 for a cogent discussion of the first two issues). Several research programs are actively engaged in answering

the first three questions [see for example papers in Box & Gibson 1999, Frigaszy & Perry 2003a, Heyes & Galef 1996, as well as the special issue of *Learning and Behavior* (2004; vol. 32, number 1) devoted to social learning]. The latter question ("How is social learning adaptive?") remains difficult to answer in an empirically rigorous way, although it is the topic of frequent speculation. Clearly the social learning of new foraging strategies improves the efficiency of foraging, and perhaps opens up new resources that would otherwise be unavailable (e.g., Boesch & Boesch 1990). Some scholars have proposed that social learning may aid primates in identifying predators and medicinal plants, guide choices of where to look for food, determine appropriate travel routes, define group membership, determine appropriate mating or social partners, assess rivals, and communicate about the quality of social relationships (see review in Perry 2003). **Table 1** shows a few examples of putative traditions documented (with varying levels of certainty about the role of social influence) in the four best-studied primate genera. This is by no means an exhaustive review of wild primate traditions, but the review articles cited in the table will direct the reader to most well-documented primate traditions discovered prior to 2003.

Some researchers focused primarily on how the speed and extent of cultural transmission is affected by various sorts of demographic conditions or behavior types. For example, Huffman & Hirata (2003) found no consistent effect of group size on diffusion rates, although they did find that innovations regarding food type and experimental tasks spread more slowly than do play and food-processing innovations. Similarly, van Schaik & Pradhan (2003) created a model that suggests that group size has very little impact on the likelihood of social transmission. Other researchers emphasized how factors such as the rate of environmental change, the cost of acquiring a trait by trial-and-error learning, and the relative reliability of social versus asocial cues would affect the tendency of

animals to engage in social learning (see reviews by Dewar 2003, Laland 2004, Laland & Kendal 2003, Richerson & Boyd 2004). These topics were also pursued by empirical researchers of birds, rodents, and other species (see for example Frigaszy & Perry 2003a). But the most quintessentially primatological topic to emerge during this time period was the study of how personality factors, emotions, and the quality of social relationships influence the probability that social learning will occur. Nonhuman primates, like humans, exhibit considerable interindividual variation in personality types and emotional expression, and they live in complex societies in which social relationships are often sharply differentiated (Aureli & Schaffner 2002, Capitanio 2004). For these reasons, it seems logical to assume that not all pairs of individuals are equally likely to learn from one another, and a good understanding of the social dynamics of a society will enhance our understanding of the dynamics of cultural transmission.

The Japanese primatologists recognized early on that there must be some link between factors such as personality, social dynamics, and the effectiveness of social transmission (Imanishi 1957). This early work was inspired by a Freudian theoretical framework rather than a socioecological one (the field of socioecology had yet to be created) and was supported more by case studies and anecdotes (as is typical in psychoanalytic research) rather than by more systematic quantitative tests of hypotheses. Imanishi's writings were somewhat vague on the mechanics of how identification (the "mechanism for introducing culture into personality") worked, and his assumptions regarding young animals' choices of role models (i.e., that cultural traits were learned almost exclusively from the mother and from the "leader male") were not rigorously tested. Kawamura (1959) also emphasized the importance of troop-specific attitudes as key factors determining the ease of social transmission and the importance of relationship quality in predicting the probability of transmission. He noted that the

Table 1 Examples of putative primate traditions in various behavioral domains

Genus	Food processing technique	Food choice	Interspecific interactions; hunting techniques	Courtship signal	Other communicative signal	Self-care	Other
Pan (Common chimpanzees, bonobos) ^{a,b,c}	Nut-cracking with hammer and anvil; termite sticks			Leaf clipping	Leaf clipping; hand clasp grooming; different display styles	Rain hats; toothpicks; nest covers (bonobos)	
Pongo (orangutans) ^d	Stick tools for <i>Nesia</i> seed extraction or to probe treeholes; leaf gloves		Loris eating		Kiss squeaking	Scratching sticks	Raspberry sound during nest building
Cebus (capuchins) ^{e,f}	Nut cracking with hammer and anvil		Squirrel neck biting; army ant following		Handsniffing; "games"; eyeball poking; sucking body parts		
Macaca (macaques) ^{g,h}	Potato and wheat washing	Fish eating		(various)	Begging gesture	Louse handling techniques	Stone handling

^aWhiten et al. 1999.

^bIngmanson 1996.

^cHohmann & Fruth 2003.

^dvan Schaik et al. 2003.

^eOttoni & Mannu 2001.

^fPerry et al. 2003b and S. Perry, unpublished data.

^gTani & Nishimura 1973.

^hsee review of wild monkey traditions (Perry & Manson 2003).

monkeys of some troops were far more relaxed around humans and also more curious about novel items being held by their group-mates, and those groups exhibiting more open attitudes were more likely to acquire and transmit new behaviors such as the adoption of novel dietary items. Kawamura, like Imanishi, thought that the social organization contributed to the acquisition of a basic attitude that was then adopted (somehow by social transmission) by all group members (Itani & Nishimura 1973) and that this attitude facilitated or inhibited social-learning processes. Subsequent work by researchers working with Japanese macaques were attentive to factors such as kinship, rank, class, and centrality in the group's spatial structure when describing patterns of social transmission [see Itani & Nishimura (1973) for an English review of this literature]. Itani emphasized the importance of knowing the history of experiences for the members of each troop: For example, history of provisioning can have a profound effect on the openness of monkeys to trying new foods (Itani & Nishimura 1973). The patterns that emerged were fairly complicated, such that it was not possible to make strong generalizations about how particular social and demographic factors influenced social transmission; rather, the type of cultural trait (e.g., food choice, food processing, play-related behavior) had a strong impact on the transmission speed, the type of innovator, and the pathway by which social transmission occurred (e.g., by mother to offspring, from peers to peers, etc.) (Huffman 1996, Huffman & Hirata 2003). This makes sense because no one individual is likely to be the most knowledgeable and skilled performer of all types of behaviors, nor do all group members have the same needs regarding the sorts of behaviors that are appropriate for them to learn at a particular time in their lives. A more sophisticated and flexible social-learning strategy is expected that takes into account the observer's current knowledge and skills, the availability of asocial cues for learning the necessary skills, the skill level and tolerance levels of avail-

able models, and the specifics of the task itself (Laland 2004).

After a long gap in which there was very little further discussion of the role of personality and social dynamics in social transmission processes, an important theoretical paper was published emphasizing that "more extensive and more frequent behavioral coordination in time and space will be achieved among groups exhibiting an egalitarian or tolerant style of social dynamics" (Coussi-Korbel & Fragasz 1995, p. 1446) and that such behavioral coordination is presumed to enhance the effectiveness of social learning. If two individuals can relax in one another's presence without one fearing domination or food theft by the other, then there is more opportunity for the animals to associate frequently and to concentrate on learning a new task in one another's presence. The idea that the quality of social dynamics affects the probability of social transmission began to receive more public recognition in anthropology when Boesch & Tomasello (1998) published their theories regarding the relationship between social structure and social transmission processes. For example, they emphasized that the extent to which social relationships are differentiated (i.e., extreme variation in the quality of relationships between dyads) is expected to affect the homogeneity of cultural traits. Also, the extent to which the social structure is egalitarian is predicted to affect the degree to which some group members can impose social norms on others, which in turn will affect the homogeneity and patterning of cultural transmission. In 1999, van Schaik et al. published their model of the evolution of material culture. One of the central tenets of the van Schaik et al. model was that both gregariousness and interindividual tolerance during foraging activities are necessary for a tool use innovation to be propagated. Thus far, the van Schaik et al. model has been tested only in a broad-strokes sort of way, for example, by doing cross-site comparisons in which mean party size is used to predict the number of feeding traditions at a particular site (van Schaik

2003, van Schaik et al. 2003). No attempt has been made to do the far more time-consuming exercise of investigating within-group diversity of relationship quality, with direct measures of tolerance, and its effects on social transmission. However, this task is currently being undertaken at my field site for white-faced capuchins, as well as by experimental researchers working on social learning in captive brown capuchins (K. Bonnie and F.B.M. de Waal, personal communication).

CULTURAL PRIMATOLOGY AND CULTURAL ANTHROPOLOGY: PROSPECTS FOR MUTUAL INFLUENCE

One of the virtues of the theoretical orientation of cultural primatology that could profitably be imported into cultural anthropology is the tendency to examine multiple levels of explanation (following Tinbergen 1963) for the existence of culture (Fragaszy & Perry 2003b, McGrew 1998). An ethologist studying culture from Tinbergen's approach would ask such questions as the following:

1. Proximate level of analysis: By which mechanisms are cultural traits transmitted from one individual? Which factors enhance or inhibit the social transmission of information or skills?
2. Developmental level of analysis: Over the lifespan of an individual animal, how are new behavioral traits acquired? (e.g., To what extent is social learning involved in the acquisition of new behavioral traits, and from whom is the animal learning these traits?) Which factors speed the acquisition of socially learned traits?
3. Phylogenetic level of analysis: What is the evolutionary history of culture? To what extent was the human form of culture present in our ancestors and our closest living relatives (i.e., the great apes)? Looking across a broad taxonomic range, in what taxa do we see human-like social-learning abilities,

and what can this taxonomic distribution tell us about the evolution of culture?

4. Ultimate or adaptive level of analysis (i.e., the typical genetic consequences of engaging in a particular behavior): What is culture good for? What is the adaptive value of having and employing social-learning mechanisms? Under which circumstances is it adaptive to rely on social cues as opposed to asocial cues for making behavioral decisions?

Cultural primatologists and other ethologists have addressed all these questions, whereas cultural anthropologists have tended, throughout the history of the discipline, to focus on a different set of questions. Cultural anthropologists have focused more on the patterning of cultural elements across culture groups (a topic rarely addressed by cultural primatologists, although see Whiten et al. 1999 and van Schaik et al. 2003 for some quite preliminary explorations in this direction). The early diffusionists were interested in how cultural elements were patterned geographically (e.g., Ratzel 1896–1898) and in the way core cultural elements cohered into “worldviews” (Frobenius 1933) or trait complexes (Herskovits 1926). Other scholars, including many archaeologists (e.g., Flannery 1972, 1973) and linguists (e.g., Croft 2000; Labov 1994, 2001; Thomason & Kaufman 1988) examined cultural macroevolution—e.g., the phylogeny of languages and horizontal diffusion of linguistic traits. Ratzel, for example, discusses how migrations and conquests by one ethnic group or another influence cultural diffusion. In this early work, the emphasis was on cultures or cultural traits as the unit of analysis, and the issue of how individual actors come to adopt the customs of their culture was ignored. Later anthropologists such as Kroeber (1963) and Gluckman (1955) emphasized culture change as a product of internal sociopolitical changes rather than being primarily a product of contact between culture groups. The emphasis on

cultural traits as the unit of analysis is shared by biologically inspired research on memetics (see papers in Aunger 2000 for a critical evaluation of the “meme” concept). Although there is much to be gained from such an approach, it is important to realize that cultural traits do not have a life of their own; they are expressed and transmitted by individual actors, who vary in interesting ways according to their psychological characteristics, developmental histories, and positions in a social network. Both the properties of the “memes” (or cultural traits) and the properties of the individual actors are important when considering the probability of cultural transmission.

Only relatively recently in the history of anthropology have anthropologists begun to localize cultural concepts in the minds of individuals and to consider which factors might make some concepts and practices more stable and transmissible than others. Cognitive anthropologists [e.g., Atran (1990), Boyer (1999), Sperber & Hirschfeld (2004)] discuss this issue at length, as do many linguistic anthropologists [see, for example, Blevins (2004) for proximate and developmental factors affecting the transmission quality of phonological traits, and also references cited in Richerson & Boyd (2004)]. In addressing this issue of the interface between the psychology of learning and the characteristics of cultural traits, cultural primatology is of most use to anthropology generally. Researchers such as Whiten (2002), Tomasello (1999), and Greenfield (Greenfield et al. 2000) have done comparative work with both humans and nonhuman primates examining the cognitive processes involved in social learning. Although our understanding of the specific mechanisms involved in learning is still far from perfect (see above), much headway has been made in determining the similarities and differences between species in their social-learning capacities and also in determining the factors affecting within-species variation in the contexts in which individuals depend on particular types of social cues. New research on the neurobiology of social learning (e.g., work on

mirror neurons, which fire both when an action is observed and when it is performed) will no doubt enhance our understanding of the proximate mechanisms underlying social transmission (Williams et al. 2001).

The second important contribution of cultural primatology is the focus on how social and ecological variables (such as those to be described in the final section of this review) affect individuals’ tendencies to adopt particular sorts of cultural traits and the focus on how social dynamics affect diffusion of cultural traits. Scholars presume that relationships between these variables will hold in humans as well as in nonhuman primates. Very little work has been done on the precise way in which different relationship qualities and interaction styles (such as tolerance of the teacher or model, history of cooperation and hence trust between the model and learner, dominance style, and mutual emotional engagement/joint attention during the activity) affect the ease of social transmission in humans. However, evidence from studies of Italian schoolchildren demonstrates that early prosocial behavior in humans (whether rated by self, peers, or teachers) is a better predictor of academic performance than is prior academic performance or aggressive tendencies (Caprara et al. 2000). It is not clear which components of prosocial behavior cause this enhancement of sociocognitive abilities. It is extraordinarily difficult to obtain longitudinal data on the details of social dynamics, personality factors, and learning opportunities (not just of academic skills but also of the skills important for daily life) over the course of an individual’s development. The fission-fusion nature of human society and the strong objection that privacy-valuing humans exhibit to being followed constantly by a researcher make these sorts of data hard to collect. Although such data are time consuming to collect in any species, it is easier to collect them in nonhuman primates than in humans. Because they share many of those human characteristics that are critical for the emergence of culture, nonhuman primates can provide a

useful model for explaining which factors promote social transmission.

Cultural primatologists and cultural anthropologists alike would do well to think more about the role of emotions in facilitating cultural transmission. The subfield of cultural anthropology known as psychological anthropology has addressed this issue in ways that are roughly analogous to the way Japanese primatologists looked at personality and culture. However, psychological anthropologists have used a variety of approaches to study the relationship between personality and culture, some focusing more on individual decision making and others focusing more on broader cultural patterns and culture-specific personalities (see Bock 1988 for a review of the early history of this field). Clearly the types of emotions displayed by models influence the amount and quality of attention they receive from observers, which affects what they learn. Emotions are likely to be particularly important in establishing social norms, in which case the type of emotional display affects the way the two participants in an interaction respond to one another. For example, conformist transmission in humans is likely to be emotionally mediated via shame (Fessler 1999): People are ashamed to be different or to be ridiculed by others, and this simple mechanism is important in giving rise to all sorts of traditions that are seemingly arbitrary, such as which hand to hold your fork in. Shame, pride, and the self-righteousness associated with punishing people for not conforming to social norms may be essential for creating the cultural complexity we see in humans. These emotions are thought to be lacking in nonhuman primates (Fessler 1999), and this lack may explain (proximately and phylogenetically) some of the differences between human cultures and simpler nonhuman cultures. Another factor that may be important in differentiating nonhuman cultures from human cultures is the prevalence of prestige-biased transmission in humans (Henrich & Gil-White 2001); prestige (freely conferred deference based on respect, as opposed to

dominance, which is deference due to fear of aggression) is likely a phenomenon that is rare or nonexistent in nonhuman primates, although this is a relatively unexplored area of research in primatology (but see Ottoni et al. 2005). The range of emotions possible in a species may be correlated with the types of cultural transmission, social complexity, and cultural complexity that are possible.

And what can cultural primatologists learn from cultural anthropologists? Cultural anthropologists have always emphasized the importance of historical perspective. Cultural primatology is such a new field that very few currently ongoing studies can claim to have a historical perspective on culture change [although Huffman's (1996) study of stone handling in macaques and the study by Perry et al. (2003a) of the appearance and dissolution of social conventions in capuchins are a step in the right direction]. Primatologists who have studied culture should, research resources permitting, maintain long-term data collection on these topics in the same populations to add a temporal component to their studies. Another important contribution by cultural anthropologists is the emphasis on the patterning of cultural elements [i.e., the study of how certain cultural elements seem to co-occur consistently owing to an underlying symbolically based ideology (Frobenius 1933) or for functional reasons (Harris 1979)]. For example, a particular subsistence style (e.g., horticulture or pastoralism) and its associated technologies tend to co-occur with a particular descent system (e.g., matrilineality or patrilineality) and a particular religion that contains symbolic elements that help organize and reinforce that descent system. Among the most striking differences between human culture and nonhuman primate traditions, given our current understanding of these issues, are (*a*) the difference in the degree to which symbolic communication is inherent in the cultural traits and degree to which cultural traits are clustered around a conceptual core, (*b*) the degree to which active teaching is part of the social transmission

process in humans (although it is important to consider the possibility that active teaching plays a more important role in Western cultures than in other human populations), and (c) the extent to which human culture is cumulative—i.e., that new cultural variants are modifications of past cultural variants rather than brand new innovations (Richerson & Boyd 2004, Tomasello 1996, Whiten et al. 2003). Although these differences are important, it nonetheless seems that humans and nonhuman primates have much in common regarding their social transmission processes and that further comparative work will be crucial to understand the evolution of human cultural capacities.

A WORKING MODEL OF HOW CULTURAL TRAITS ARISE

Here I present a model (**Figure 1**) of how most (or at least many) cultural primatologists conceptualize the process of how cultural traits are formed and maintained in nonhuman primates and humans. Although this model has not been presented in its entirety in any other place, work by other authors has developed particular links in this model, as articulated earlier in this paper. Of course, many other aspects of the cultural process have been omitted from this model—for example, I have not explicitly discussed gene-culture coevolution here. The reason is because this topic has not yet been addressed empirically in nonhuman primate studies; nor do I know of any researcher who has imminent plans to do so. A complete model of cultural processes would, of course, have to integrate genetic feedback (Richerson & Boyd 2004).

Basically, cultural primatologists are interested in how external variables (i.e., aspects of the physical and social world) affect particular psychological attributes of animals (i.e., attitudes toward particular tasks and individuals, and also mental representations of particular actions), which in turn affect the tendency for them to exhibit behavior patterns that are either similar to, or different from, the behav-

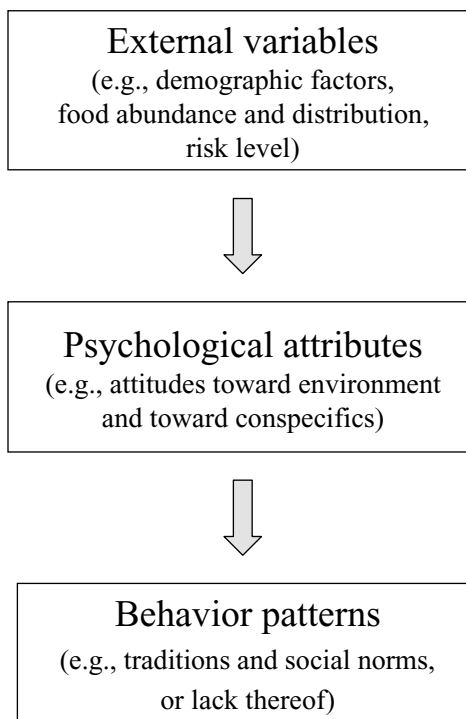


Figure 1

Model of factors affecting the propensity to develop traditions and social norms.

iors of their groupmates in similar contexts. The external variables can exert an effect on psychological attributes and behavior on an evolutionary time scale (via natural selection) and/or on an ontogenetic time scale. Let me first describe in more detail what I mean by each of these three categories and then give some specific examples of how particular sorts of traditions and social norms could arise.

The sorts of external variables I have in mind consist primarily of those variables that have long interested primate socioecologists: aspects of the demography and ecology of the animals. For example, variables such as sex ratio, group size, birth cohort size, and the ratio of adults to immatures in a group will affect the number and type of models from which any particular individual can learn. Availability of models is likely to affect the probability and speed of social transmission of traits, as well as the patterning of the spread

of the trait through the group. Ecological variables of interest include food abundance, distribution, and diversity. Variables such as food abundance and distribution influence aspects of primates' social relationships, such as tolerance, dominance style, and propensity to cooperate (van Schaik 1989, 1996). The degree of risk in the environment (e.g., prevalence of exposure to toxins, predators, and dangerous conspecifics) is likely to affect individuals' levels of caution in testing new foods or interacting with unknown animals, which in turn could affect their abilities and propensities to learn about novel foods or animals via asocial means (trial-and-error learning). Another potentially important influence on group dynamics that has not so often been considered is the role of individual personalities, and particularly the personalities of long-term alpha males and females, who set the tone for how tolerant group dynamics can be, in general. To give an example, the successive alpha males of one of my capuchin groups consistently engage in separating interventions, punishing attempts by other males to associate with one another. In contrast, the males of some of my other groups are tolerant of other males' affiliations, such that these males are free to associate and cooperate frequently, and the group has a more relaxed social atmosphere overall. Such influences could persist even after the death or emigration of the animal(s) whose personality created the norm, as in Sapolsky & Share's (2004) documentation of a founder's effect on a culture of peacefulness in baboons.

Psychological attributes include at least two types of phenomena: (*a*) attitudes (e.g., emotional responses to particular types of situations) and (*b*) mental representations of tasks. The first, attitudes, is of primary interest to socioecologists interested in determining how external variables such as those discussed above translate into patterns of behavioral responses because some attitudes are more conducive to social learning than others. Examples of attitudes are tolerance, neophobia, and emotional engagement (high interest level in

an object, task, or individual animal). Tolerance has been hypothesized to enhance the probability of social learning (Coussi-Korbel & Frigaszy 1995, van Schaik et al. 1999). Neophobia decreases the odds that an animal will learn about a new food by trial-and-error learning. Strong expression of emotion by models toward the objects with which they are engaged increases the salience of objects to the observer such that observers are more likely to explore the objects (Fragaszy et al. 2004). And high emotional engagement between participants seems to be a critical feature of traditional bond-testing rituals in capuchins (Perry et al. 2003a) and interaction rituals in humans (Collins 1993). It seems clear that emotions add salience to learning situations, focusing the observer's attention on particular aspects of its environment. Being sensitive to the emotional states and gaze directions of others enables joint attention of the model and the observer on the same aspects of an activity pattern, thereby enhancing the probability that some aspect of the model's knowledge and/or behavior will be acquired by the observer.

The second type of psychological attribute, mental representations, refers to the animal's conceptualization of (*a*) a particular object's properties, (*b*) a particular course of action, (*c*) a cause-and-effect relationship between two objects or individuals, or (*d*) a particular type of social interaction. For one individual to learn socially from observing a demonstrator's actions, the observer will have to produce a mental representation that is at least partially overlapping with the demonstrator's mental representation of the task, although the degree of overlap may be very slight (Richerson & Boyd 2004). It is this particular black box that most concerns those cultural primatologists who do experimental work to discern the precise social learning mechanisms employed by primate species in specific contexts. Of course, it is quite difficult to know what mental representations are present in animals' minds because the only clues we have are their behavioral outputs.

Typically when one primate observes another performing some task and learns socially from these observations, it does not exhibit a perfect replication of what it has observed, which implies that the primate is not conceptualizing the task in exactly the same way as the model. The aspects of a behavioral sequence that seem salient to one observer may not be the same aspects that are salient to another. To give a hypothetical example, if three animals were watching a fourth conspecific crack open nuts with a stone and eat them, one might learn from this observation that nuts are good to eat, the second might learn that combining uncracked nuts and stones produces cracked nuts (without appreciating the importance of the specific motor actions involved), and the third might learn that the specific act of pounding yields food (but may fail to understand why a stone is a particularly good item to pound with). All three of these observers might take the different bits of information they acquired from watching the model and then modify those mental representations with further information acquired from subsequent trial-and-error learning, until they devised their own subtly different techniques for opening nuts. It is devilishly difficult to know exactly how an animal conceptualizes its understanding of a particular task and the exact extent to which one animal's mental representation overlaps with another animal's. But it is important to understand that even if two animals have only partial overlap in their mental representations, they can converge on similar or identical behavior patterns such that a tradition is formed.

Finally let us consider the behavioral patterns that cultural primatologists are trying to explain: traditions and social norms. I define a tradition as a relatively long-lasting behavior pattern shared by multiple practitioners owing to some form of social learning. Most of the traditions that have been studied by cultural primatologists consist of readily identifiable, discrete behaviors (e.g., quirky foraging techniques such as nut cracking or potato washing) that can be reliably coded as present

or absent in a particular individual. Foraging techniques, and material culture in particular, have been a focus of study both in humans and nonhumans because of the ease with which such traits can be identified. But there is another whole type of behavioral patterns, which consists of group-typical responses to particular social situations, that can perhaps be defined best as social norms. Such behavior patterns would technically fit my definition of tradition because of the role of social learning in their establishment, but I distinguish them from traditions merely because they are harder to identify and operationalize. Social norms are patterns of social behavior that typify particular groups and are variable between groups, but which each individual within a group can follow to varying degrees, such that it is difficult to classify any particular individual as possessing or lacking the trait. The acquisition of social norms is directly influenced by social interaction with others but not necessarily by copying what has been observed: The process of internalizing a norm could come about by taking a complementary role in an interaction rather than by adopting the same role as the model. Although the term social norm would imply punishment for violation of a social rule to many scholars, that condition is not a necessary part of my definition for the purposes of this discussion.

A well-documented human example of a social norm is the culture of honor in the southern United States, in which southerners are far more polite than northerners in general but also are far more likely to respond to insults with extreme physiological stress responses and impulsive violence (Nisbett & Cohen 1996). Some nonhuman primate examples of social norms would be peacefulness in the forest baboon troop of Masai Mara (Sapolsky & Share 2004) and matrilineal inheritance of dominance rank in macaques, in which a monkey socially inherits the rank just below her mother and just above the older sister that is closest to her in dominance rank (Chapais 1988). Some primatologists have produced experimental evidence for

social norms. For example, rhesus macaques (*Macaca mulatta*) rarely reconcile, yet when de Waal & Johanowicz (1993) housed rhesus juveniles with juvenile stumptail macaques (*M. arctoides*), which reconcile far more frequently, the young rhesus developed a stumptail-like reconciliation rate that persisted after the rhesus were placed back in all-rhesus groups. Yet the rhesus juveniles did not acquire species-typical stumptail reconciliation gestures, suggesting that social attitudes rather than motor patterns were transmitted between individuals of the two species. Also, Kummer (1996) found that female hamadryas baboons (which are accustomed to exclusive relationships with a single male) can quickly adapt to the different consort style of savanna baboons (in which male-female sexual relationships are more fluid and transient and males are less controlling) and vice versa when females from one species are transplanted into groups of the other species.

Further possibilities for cognitive rules in primates in which the role of social learning may prove to be influential are the acquisition of decision rules determining which animal to side with in a coalition (Perry et al. 2004) or the tendency to punish certain behaviors. Social norms are slowly established over time, as maturing animals or immigrants adjust their behaviors in accordance with the behavior patterns exhibited by the majority of animals (or, perhaps, with the behavior patterns exhibited by particular influential animals). Because an individual is unlikely to conform to the norm in 100% of its opportunities to do so, it

is difficult to say with certainty when any particular animal has internalized a social norm. Likewise, it is hard to say at a group-wide level when a social norm has been clearly established. For these methodological reasons, and for the reason that vast amounts of behavioral data are necessary to document changes in social norms over the history of a group or in the course of an individual's ontogeny, very few primatologists have devoted research effort to studying social norms. Nonetheless, they are a fascinating topic of inquiry and one that is likely to shed light on the origins of human culture (de Waal 2004). Although most of the empirical anthropological work on the dynamics of human culture change has also focused on material culture and subsistence technology (Richerson & Boyd 2004), perhaps for the same methodological reasons that have created this research bias in cultural primatology, the most profound and subtle aspects of cultural variation clearly center around differences in status relations and appropriate means of negotiating social relationships in a complex society. Although much human relationship negotiation employs symbolic communication in the form of language, many aspects of human social norms consist primarily of gestures, postures, and appropriate behavioral coordination in space and time (for example, culture-specific ways of greeting a socially dominant individual or of resolving a conflict). Social norms of these types may prove not to be so different from social norms in nonhuman primates.

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