
Chimpanzee and Human Cultures

by Christophe Boesch and Michael Tomasello

Culture has traditionally been attributed only to human beings. Despite growing evidence of behavioral diversity in wild chimpanzee populations, most anthropologists and psychologists still deny culture to this animal species. We argue here that culture is not monolithic but a set of processes. These processes show much diversity both in the social norms and models that determine which individuals will be exposed to particular cultural variants and what cultural variants will be present in the population and in the social learning mechanisms that determine the fidelity of transmission of the variants over time. Recognition of the diversity of these processes is important because it affects cultural dissemination, cultural evolution, and the complexity of cultural artifacts. A comparison of chimpanzee and human cultures shows many deep similarities, thus suggesting that they share evolutionary roots. Two possible differences between the two species are discussed. First, thanks to indirect means of transmission such as language, cultural dissemination is possible over greater stretches of time and space in humans than in chimpanzees. Second, human cultures rely more intensively than chimpanzee cultures on cumulative cultural evolution through the ratchet effect, which allows the accumulation of modifications over time and produces more elaborate cultural artifacts.

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There is little agreement among anthropologists on precisely what is meant by the term "culture" as it is applied to human social groups (e.g., Kroeber and Kluckhohn 1952, Shore 1996). It might be supposed that looking to nonhuman primate societies for the evolutionary roots of human culture would simplify the definitional problems involved, if only because primate societies are not expected to include such ideal entities as values, attitudes, and beliefs, whose role in culture has been the main point of contention in many anthropological debates. Unfortunately, this is not the case, even though evolutionary biologists and comparative psychologists interested in culture have been primarily concerned with seemingly straightforward processes of social learning and other forms of nongenetic information transfer among members of social groups. The main problem is that the different disciplines involved approach the problem of culture with different sets of concerns. The basic dichotomy is between biological approaches, in which all information that is transmitted nongenetically among members of a group is of interest (e.g., Bonner 1980, Boyd and Richerson 1985, Dawkins 1976, Cavalli-Sforza and Feldman 1983, Munding 1980), and more psychological approaches, in which the main concern is the cognitive and learning mechanisms by means of which such information is transmitted (e.g., Galef 1992, 1996; Tomasello 1990, 1996).

These two approaches may be illustrated with the well-known case of the potato washing of a group of Japanese macaques (Kawamura 1959, Kawai 1965). A young female of this species discovered a new and useful food-processing technique with human-provisioned potatoes that had become sandy, and this behavior spread quickly—at least in the context of evolutionary time—to other group members, possibly as they imitated one another's behavior. The researchers documented in meticulous detail which individuals acquired the behavior and when they acquired it, establishing, among other things, that (1) the relatives and close associates of the original inventor acquired the new behavior first and (2) adult males generally did not acquire the new behavior at all. From a biological point of view, an acquired skill—and one that would seem to be at least somewhat instrumentally useful—was transmitted among individuals of a group and contributed to improved methods of foraging. On the basis of the general similarity of this process to human cultural transmission, Japanese macaque potato washing has been taken as a textbook case of cultural transmission that illustrates the deep evolutionary roots of human culture.

Recent reanalysis and reinterpretation of these observations from a more psychological perspective, however, have also highlighted some possible differences of this case from the human case. Galef (1992) reanalyzed the original data and suggested that individual Japanese macaques most likely learned to wash potatoes on their own (as had the original inventor), not by imitating their groupmates. As evidence for this view he noted

that the spread of the behavior was relatively slow, with an average time of over two years for acquisition by the members of the group that learned it (approximately half)—which would not seem consistent with a process of imitation (typically assumed to be more rapid). Moreover, the rate of spread did not increase with the number of users as would be expected under the imitation hypothesis as more demonstrators became available for observation across time (but see Lefebvre 1995 and our models below). Galef also noted that after a certain period many youngsters grew up following their mothers into the water and finding potatoes there, an excellent opportunity for individual learning and discovery, and, indeed, Visalberghi and Frigaszy (1990) found that other macaques could learn this behavior on their own quite rapidly if provided with sandy fruits and bowls of water. The point is that in Galef's interpretation the spread of the behavior was due not to imitation but rather to each individual's "reinventing the wheel," with the behavior of those who had already acquired it creating propitious learning conditions for those who followed. The transmission process in this case would thus seem to be somewhat different from that involved in at least some human cultural traditions, which have been shown to rely mainly on individuals' imitating one another's behavior or behavioral strategy (e.g., language).

In this paper our focus is on chimpanzee culture and cultural transmission, with an eye to both similarities to and differences from the human case. We focus on the chimpanzee because, of all the 180+ species of primate, it is clearly the most interesting from a cultural point of view. To a degree unknown in any other species of nonhuman animal, primate or otherwise, different populations of chimpanzees seem to have their own unique behavioral repertoires, including such things as food preferences, tool use, gestural signals, and other behaviors, and these group differences often persist across generations (see McGrew 1992; Boesch 1996a, b, and the papers in Wrangham et al. 1994 for recent reviews). From the biological point of view, there is no question that much of chimpanzee behavior is culturally transmitted in the sense that individuals consistently acquire behaviors specific to their population in ways that do not depend directly on genetic transmission or upon obvious ecological conditions (e.g., Boesch 1996a, b). From the psychological point of view, however, it is possible that in some cases the population-specific behavioral traditions of chimpanzees are due to each individual's adapting individually to its own local environment—eating only the foods that are locally available, to give a mundane example—with the social environment playing a minor role in the acquisition process (Tomasello 1990, 1994), whereas in other cases one of several processes of social learning and imitation may be at work.

Our central theoretical point in this paper is that culture is not monolithic. We begin with an evolutionary perspective on patterns of cultural behavior in different chimpanzee communities in the wild, detailing some of the population-specific behaviors known in this spe-

cies. We proceed to show that in general within one population there are many possible social conditions and lines of dissemination through which individuals may be exposed to particular behavioral practices within communities. We then show that there are many different types of social learning processes by means of which individuals may acquire these behavioral practices, and these different learning processes lead to cultural traditions with different properties over time. In this context we introduce some recent research on the social learning of captive chimpanzees. We conclude with an explicit comparison of chimpanzee and human cultures.

It is perhaps of special note that in the past the two of us have been somewhat at odds on the question of chimpanzee culture and its relation to human culture (e.g., see Tomasello, Kruger, and Ratner 1993 and Boesch 1993, 1996a, b). This paper represents our attempt to reconcile at least some of our theoretical differences and to locate more precisely the differences that remain in an attempt to guide future research on the question of chimpanzee culture toward the most pressing and important theoretical issues.

Population-Specific Behaviors in Chimpanzees

Humans and chimpanzees, along with many other animal species, acquire their behavior via processes of genetic transmission, individual learning, and social learning, with the precise contribution of each of these sources of information differing for different behaviors. As a means of information transfer, genetic transmission occurs once per reproductive event and produces relatively inflexible behavior—and it produces this behavior according to the Mendelian rules of inheritance in the descendants of one individual (Ridley 1996). Individual learning can occur more rapidly than genetic transmission, as each individual may learn many new behaviors during its lifetime. Population-specific behaviors based on individual learning have been observed in a wide variety of animals where individuals adapt to their local physical environments. This kind of individual learning influenced by local ecology—and thus leading in some cases to population differences in behavior—is generally not considered cultural transmission because the social environment is not involved. Galef (1992) has called it "environmental shaping." Social learning and the resulting cultural transmission may also occur independent of reproductive events and more than once in a lifetime. Social learning may sometimes be even more rapid than individual learning, because individuals may learn by observing others.

For current purposes we may posit that the naturally occurring behaviors of a primate group may be assumed to be cultural (i.e., due primarily to social learning) when (1) two groups of the same species differ in a behavior (with a countable number in each group con-

forming), (2) there are no obvious differences in the environments of the two groups, making an explanation in terms of individual learning (environmental shaping) unlikely, and (3) there are no genetic differences between individuals that acquire the behavior and those that do not.

A description of some population-specific behaviors found in wild chimpanzees will illustrate the range of cultural potentialities demonstrated by these animals and serve as a base for our discussion on the social aspects of cultural transmission. The list in table 1 is not exhaustive; we have limited it to the longest-studied

populations because it is only in these cases that we can know the whole repertoire of a population. Published material on all tool uses and other behaviors is available only for the chimpanzees of Bossou, Gombe, Mahale, and Taï. The difference between four thoroughly studied chimpanzee populations and, for example, some 650 distinctive human societies used for a study of war (Wright 1942) is a measure of how little we know about our closest living relative. Also not listed in table 1 are all the population-specific behaviors for which a clear ecological explanation could be provided to explain the irregular distribution within the species. A comparison with figure 1, which shows the geographical distribution of those populations throughout Africa, gives an idea of the variation in the distribution of the behaviors. Table 1 is incomplete also because no systematic comparative study in the field has attempted to discover all the potential cultural behaviors in this species.

Are all these behaviors group differences rather than individual differences? It is not always possible to tell from the literature how many individuals performed a given behavior, but there is no doubt that the ones we shall discuss in detail are group differences. Since we have been following the Taï chimpanzees we have identified 123 individuals, and all those that were old enough to crack nuts did so regularly; a single juvenile female never did so, probably because two badly handicapped hands prevented her from holding a hammer (Boesch 1991). As we shall see later, we should not expect all group members to perform all population-specific behaviors, because social constraints may limit their distribution within a population. For example, leaf clipping in Taï was practiced for years only by adult males but by all of them. As adult males represented only about 10% of the community, a minority of the group members were practicing leaf clipping. However, it seems to us that this is not individual behavior but the distinctive behavior of a particular social category. This is also observed in many human cultural patterns, where a behavior is performed only by individuals of a certain age or social category. Similarly, ant dipping was mainly a female activity but was nevertheless seen in about 80% of Taï adult group members and in 29 adults at Gombe (McGrew 1974, 1979). Termite fishing at Gombe was also predominantly a female activity but has been reported in all adults of the Kasakela community (McGrew 1977, 1979). Squashing of ectoparasites on leaves was seen in 24 individuals at Gombe, while at Taï most group members squashed them on their forearms (Boesch 1995). Thus, when data are available these behaviors tend to be performed by a large majority of the individuals of a given class.

As we have mentioned, ecological differences in the environment inhabited by different chimpanzee populations may in some cases be a direct explanation for the variations we observe between them. For example, in West Africa, the chimpanzees of Mont Nimba (Côte d'Ivoire) were observed to bang hard-shelled *Strychnos* fruit against tree trunks to open them as do the chimpanzees at Taï and Gombe, whereas their direct neigh-

TABLE 1
Population-Specific Behaviors Documented in Wild Chimpanzees That Cannot Be Explained by Ecological Differences Alone

Pattern	Chimpanzee Population					
	Bossou	Taï	Kibale	Assirik	Gombe	Mahale
Foraging behavior with tool use						
Ant dip	+	+	-	+	+	-
Honey dip	-	+	-	-	+	-
Bee probe	-	+	-	-	-	-
Leaf sponge	+	+	+	-	+	-
Marrow pick	(-)	+	-	(-)	-	-
Nut crack	+	+	(-)	(-)	(-)	(-)
Termite dig	-	-	-	(-)	-	-
Pestle pound	+	-	-	-	-	-
Hook stick	+	-	-	-	-	-
Gum gouge	+	(-)	-	-	-	-
Termite fish	-	(-)	-	+	+	+
Algae fish	+	(-)	-	-	-	-
Communicative behavior						
Missile throw	+	+	-	-	+	+
Branch haul	+	+	-	-	-	-
Stick club	-	+	-	-	+	+
Hand clasp	-	+	+	-	-	+
Leaf clip	+	+	-	-	-	+
Play start	-	+	-	-	+	+
Knuckle knock	-	+	-	-	-	-
Leaf groom	-	-	+	-	+	+
Body-oriented behavior						
Fly whisk	+	+	-	-	+	-
Index hit	-	+	-	-	-	-
Ground nest	-	+	-	-	-	-
Leaf napkin	-	-	+	-	+	-
Self-tickle	-	-	-	-	+	-

SOURCES: Bossou, Sugiyama (1981), Sugiyama and Koman (1979), Matsuzawa and Yamakoshi (1996); Taï, Boesch and Boesch (1990), Boesch (1993, 1996a); Gombe, Goodall (1986), McGrew (1992, 1994); Mahale, Nishida (1973, 1987), McGrew (1992); Assirik (Senegal), McGrew, Baldwin, and Tutin (1979); Kibale (Uganda), Wrangham and Isabirye-Busata, cited in McGrew (1992).

NOTE: +, population in which the behavior has been observed; (-), population in which the behavior is absent but this is easily explained by the absence of the resource; -, population in which the behavior is absent and cannot be explained by simple ecological differences.

bors, the chimpanzees of Bossou (Liberia), have never been seen to do so because the *Strychnos* fruits are not available there (Matsuzawa and Yamakoshi 1996). Similarly, Tai chimpanzees often crack coula and panda nuts, whereas chimpanzees in Gombe, Bossou, and Mahale have never been observed to do so (Boesch and Boesch 1990, Goodall 1986). As the two species of nuts do not occur at Gombe and Mahale, the explanation for the behavior's absence is obvious. Such an explanation applies to only a few of the behaviors listed in table 1, however. For example, extracting bone marrow from prey eaten with a stick has been observed only at Tai and is absent at Gombe, Kibale, and Mahale, where chimpanzees regularly eat the same species of prey (red colobus monkey). However, Bossou and Assirik chimpanzees have never been seen to eat monkeys, and the absence of marrow picking there can be explained by this observation.

For nut cracking the situation is complicated by the fact that besides populations that do not crack nuts because these are absent we know of many populations living within the distribution range of the two nut species that do not crack them. This is true for chimpanzees in the forests of Gabon (Tutin and Fernandez 1984), Cameroon (Sugiyama 1990), and Ghana and central and western Côte d'Ivoire (Boesch et al. 1994). A closer analysis of nut cracking in Côte d'Ivoire revealed that the Sassandra-N'Zo River is the boundary of the behavior: chimpanzees on the east side do not crack nuts, whereas chimpanzees on the west do. Some populations on the two sides of the river are only 30–50 km apart, and the most relevant ecological factors affecting nut cracking, such as availability of nuts and tools, as well as the density of chimpanzees, can be excluded as explaining this difference (Boesch et al. 1994).

For most behaviors classified as foraging behavior it can be argued that subtle ecological differences or differences that existed in the past may be the source of population differences (Tomasello 1990). The problem is that this argument is almost impossible to disprove. However, for communicative and body-oriented behaviors (e.g., leaf clipping) such argumentation applies much less easily, as a branch or a leaf is the most that is required for behaviors using an object (10 of the 13 listed in table 1). These behaviors are thus only marginally dependent upon ecological constraints and much more influenced by social factors. At first glance they seem to be the best candidates for cultural behaviors in chimpanzees.

Population-specificity is more complicated than it first appears, since some behaviors present in many populations have been shown to differ in form or function (Boesch 1996a, b). Two behaviors, ant dipping and leaf clipping, are especially instructive in this respect. Ant dipping has been observed in four populations (table 1); however, two different techniques of dipping for ants have been observed (Boesch and Boesch 1990, McGrew 1974). At Tai, chimpanzees hold the stick with one hand and dip it among the soldier ants (*Dorylus nigricans*) guarding the nest entrance. When the

ants have swarmed about 10 cm up the tool they withdraw it, twist the hand holding it, and directly sweep off the ants with the lips. Tai chimpanzees use sticks 30 cm long on average and perform the dipping movement about 12 times per minute, taking an average of 15 ants at a time. Gombe chimpanzees hold the stick with one hand among the same species of soldier ants guarding the nest entrance and, once they have swarmed about halfway up the tool, withdraw the stick and sweep it through the closed fingers of the free hand; the mass of insects is then rapidly transferred to the mouth. Gombe tools are on average 66 cm long (range 15–113 cm), and the dipping is performed 2.6 times per minute. Thus, of the two techniques used to dip for ants one is clearly more efficient (Tai, 180 ants/min.; Gombe, 760 ants/min.). Nevertheless, all the chimpanzees belonging to a population were seen to use one and the same technique.

Leaf clipping was first described in the Mahale chimpanzees in Tanzania, as follows: "A chimpanzee picks one to five stiff leaves, grasps the petiole between the thumb and the index finger, repeatedly pulls it from side to side while removing the leaf blade with the incisors, and thus bites the leaf to pieces. In removing the leaf blades, a ripping sound is conspicuously and distinctly produced. When only the midrib with tiny pieces of the leaf blade remains, it is dropped and another sequence of ripping a new leaf is often repeated" (Nishida 1987:466). None of the leaf is eaten. Leaf clipping has also been observed regularly at Bossou (Sugiyama 1981) and Tai (Boesch 1995, 1996a, b) but only twice at Gombe (Jane Goodall, personal communication, cited in Nishida 1987). The function of this behavior differs between populations and seems arbitrary. At Mahale, chimpanzees perform it most commonly as a herding/courtship behavior in sexual contexts (23 of 41 observations [Nishida 1987]): young adult males and adult estrous females apparently performed it to attract the attention of group members of the opposite sex (M. Huffman, personal communication). At Bossou it has been observed mostly in apparent frustration or in play (41 of 44 observations [Sugiyama 1981 and personal communication]). During the habituation period individuals surprised in trees might leaf clip while watching the human observer. Once the habituation was more complete, this form of leaf clipping disappeared, and it is now observed in youngsters only as a form of play. At Tai it is in the first place a behavior performed by adult males before drumming (249 out of 321 observations [Boesch 1995]); here the situation is complicated by the fact that during the first ten years of the study all and only adult males leaf clipped just before drumming (129 out of 132 observations) but in late December 1990 the behavior suddenly began to be performed also by members of all age/sex classes and while resting (32 out of 183 observations). This evolution in the context of performance of a behavior took place within a month and affected all 6 adult males and 11 other group members (Boesch 1995).

Analogous to the arbitrary variation in the context of

leaf clipping in three chimpanzee populations, similar functions may be fulfilled by different behaviors in different chimpanzee populations (Boesch 1996a, b). Sexual courtship by male chimpanzees in all known populations is generally done by shaking a sapling while showing the erect penis to the estrous female. Younger males at Mahale may attract the attention of estrous females by leaf clipping, which is less conspicuous than the usual sapling waving. At Taï, males that may want to be inconspicuous knock branches or tree trunks with their knuckles to attract the attention of an estrous female. Similarly, chimpanzees may squash ectoparasites that they intend to eat. At Gombe chimpanzees were observed to place ectoparasites they found while grooming another individual or themselves on leaves and then squash them with their thumbs before eating them (this behavior is called leaf grooming in table 1 [Goodall 1986, Boesch 1995]). At Taï chimpanzees place the ectoparasites on their forearms and squash them by tapping them with the tip of the index finger of the other hand [Boesch 1996b]). Leaf grooming was never seen at Taï, nor was index hitting at Gombe. Here again the group seems to decide which behavior will be used to fulfill a given function, and this choice seems arbitrary.

In conclusion, population-specific behaviors in wild chimpanzee populations have been observed in different contexts, and this includes not only behaviors' being present or absent in different populations but also differences between populations in the form or the function of the behaviors performed. This pattern is not compatible with a simple ecological explanation and points to the importance of social influences in producing and maintaining these population-specific behaviors.

Patterns of Dissemination within Populations

Culture is a social phenomenon, and thus social structure can have a major influence on the dissemination of information. Social influences act at different levels at the same time, and we shall differentiate between them, starting at the highest social level and going down to that of the individual. For cultural transmission to occur, a novel behavior, the cultural variant, spreads between individuals within a group. The variant may appear in a population through innovation or immigration from other populations. However, we know from all human cultures that not all cultural variants have the same likelihood of being acquired by other group members. What determines which novelties will persist and how cultural changes spread or are lost are questions central to most theoretical discussions of the evolution of culture (Alexander 1979; Boyd and Richerson 1985; Cavalli-Sforza and Feldman 1973, 1981; Durham 1991; Flinn and Alexander 1982; Lumsden and Wilson 1981; Wilson 1978). Our present discussion will differ from previous ones in taking a plu-

ralistic approach to understanding how qualitatively different social constraints affect the diffusion and transformation of cultural variants within a population and therefore produce different cultural systems.

Cultural-variant acquisition is rarely if ever a free choice among numerous options; there are always constraints. These constraints not only determine what will be acquired but also limit the possible modifications of the cultural variants throughout their existence. For example, in the potato washing of Japanese macaques, the inventor, Imo, associated primarily with members of her maternal line, and members of other lines were therefore not in a position to copy her. Two distinct kinds of social constraints can be identified. The first determines the array of cultural variants available in the group among which a naive individual may choose. We shall call this the *social norm*. The second identifies the *social model* that naive individuals will have available to learn from in particular cases and therefore determines which variants will be acquired.

THE SOCIAL NORM

Choice of cultural variants is directly affected by what members of the group can observe. At this level, one of three groupwide conditions may prevail: free choice, convention, and imposition.

With *free choice*, all cultural variants will be tolerated by group members, and from the social perspective the cost of adopting one variant rather than another is the same. Under this condition, the number of cultural variants present in a group will be limited only by the rate of innovation by group members and the rate of introduction of new variants. Because the variants are learned from group members they fulfill the psychological notion of culture, and if the number of variants within the group is limited they will fulfill our criterion for culture.

With *convention*, only a given set of cultural variants is tolerated for the whole group, and no clustering of particular classes of individuals is observed. New cultural variants, introduced either by innovation or by immigration from other groups, will tend to be rejected and will rapidly disappear. Conventions are thought to be reinforced by the different social costs associated with using different cultural variants. Culture under this model will be more unified in the sense that most members of the different subgroups within a population will use the same cultural variants, but it remains variable because conventions may embody more than one option. An example of a convention in chimpanzees is dipping for driver ants (Boesch and Boesch 1990; Boesch 1996a, b; McGrew 1974; Goodall 1986). As we have seen, ants can be captured with the help of twigs by two different techniques requiring different lengths of tools and different movements, but each technique has been observed in only one population despite the fact that one of them is clearly less efficient (Boesch and Boesch 1990). Such conventions are considered common in human societies and have typically been attributed to

neighboring societies' differentiating themselves from each other with striking differences in dress, greeting customs, and so on.

Finally, given sets of options may be presented to group members through *imposition* by a subgroup, making cultural evolution a political process (Durham 1991). This is most clearly exemplified in the human case, where one group coerces another to adopt major changes in cultural domains (e.g., the Chinese on Tibetans or Europeans on Native Americans). Where a class of individuals forces or manipulates others into adopting certain cultural variants we will observe a culture similar to the one produced by convention, and it is the degree of homogeneity that will differentiate the two. If coercion is not entirely successful, variation will remain at a low level in individuals that resist it.

Imposition may be achieved not only by force but also by information manipulation or demonstration. In this category we think of teaching, in which a subgroup instructs or informs others to acquire a given cultural variant, thereby directly reducing the number of cultural variants available to individuals within the population. Teaching in its modern form in human societies clearly exemplifies this imposition of cultural knowledge on a large proportion of the population. The best cases of teaching in chimpanzees have been observed in the nut-cracking context at Tai (Boesch 1991).

THE SOCIAL MODEL

Within the framework of social norms, individuals will select the cultural variants they observe being performed by other group members. The differential success of behavior variants in spreading within a group indicates that not all group members are equally good as models. The benefit gained by using some variants may play a role in their dissemination, but there are enough examples of cultural behavior patterns that provide no obvious gain or that seem nonadaptive (e.g., the ant-dipping technique in Tai chimpanzees [Boesch 1996a, b] and infanticide or vendetta warfare in various human populations [Chagnon 1988]) to justify our attempt to understand the role of social models in cultural dissemination. The null hypothesis would be that individuals choose at random and that all cultural behavior patterns have the same chance of spreading (Lumsden and Wilson 1981); only chance events could lead to one of the options' becoming more prevalent and leading to a culture (this process is similar to drift in evolutionary processes [Alexander 1979, Ridley 1996]). We shall distinguish five social models that will bias the spread of cultural variants, each leading to a particular clustering of variants: individual, family, association, majority, and prestige. These models are not mutually exclusive; for a given cultural behavior several models may apply.

With the *individual* model, individuals face a free-choice situation and select the cultural variants that provide them with the greatest individual fitness (Dawkins 1976, Durham 1991, Wilson 1978). Existing cultural variants within a population will be the most

adaptive for the conditions to which this population is exposed. If most individuals face the same set of options, experience very similar social and ecological conditions, and acquire the options in a similar way, we will observe a stable and unified culture. If, as is more likely, individuals differ in some of these features, the variation within the population in terms of cultural variants observed will be too large for it to look like a culture. Under this model, it will be very difficult to differentiate between an individual and a cultural learning process, as both are expected to favor adaptive solutions.

With the *affinity* model, in contrast, individuals choose their models from among the collection of individuals that share their options and experiences. The selection of a reference group (as defined by Durham 1991) is directly influenced by the population's social structure and social rules. In our pluralistic approach, this point is substantial, because group size and composition and social organization and structure vary significantly among species and among populations of a single species (Stammach 1987, Boesch 1996b, Smuts et al. 1987). The remaining four models are all affinity models.

Under the *family* model, individuals have strongest affinities with family members, and so the choice is made among the options available within this limited reference group. Cultural changes will follow family genealogies, and cultural differences within the group will be very apparent. This is the classic example of vertical transmission of knowledge from mothers to offspring that has been documented in many animal species. An example of transmission in other directions may be the dissemination of potato washing among Japanese macaques, where older individuals acquired the behavior only if one of their offspring had acquired it and youngsters seemed to acquire it from peers (Kawai 1965).

Under the *association* model, association within a social group is not random and the reference group is selected from among those with whom the individual most frequently associates. In this case, cultural variants will be observed mainly between close associates and therefore overlap with sociograms of the group. In many cercopithecine species, association is greater between members of the same matriline, and here the family and the association model will produce the same clustering. In chimpanzees association is much less dependent upon relatedness, and the two models make different predictions.

Under the *majority* model, individuals choose the options that are being used by the majority of members of the population; they consider the cultural variants present in the group and select the ones most commonly observed. Culture will be much more unified under this model, as a single variant will rapidly reach fixation (analogous to genetic selection, fixation is observed when only one cultural variant remains in the population). In addition, innovations will spread only with difficulty in such a population.

Under the *prestige* model, individuals choose the op-

tions that are used by the members of the population that they perceive as having the most prestige. Prestige may, however, vary for each individual within a population and over time. We will tend to expect similarities that are socially structured; for example, lower-ranking individuals will tend to choose higher-ranking individuals and young hunters will select gifted hunters as models. This process will lead to elaborate clustering in the population's cultural system.

These four affinity models will produce different distributions of cultural variants within the population, and this may theoretically allow us to discriminate among them. However, as we have said, they are not mutually exclusive. In the example of the Japanese macaques, both the family and the association model may have been at work. The slow acquisition of this behavior has made it possible to see these patterns, but once fully acquired it would be difficult to differentiate the combined effect of the two models from that of a majority model. It remains important, however, to differentiate between these models, because there is no a priori reason to believe that all cultural systems in animal and human populations will make equal use of all of them.

Social norms and social models are often combined, and social constraints on both levels have as their main effect reducing the rate of cultural change (table 2). For example, we may find within a single population a majority model that blocks all variants for a feeding habit, a prestige model for greeting gestures that allows few variants, and an individual model for food calls, and here both rapid and very slow cultural changes will be expected. This exemplifies the risk associated with using rate of cultural change as a criterion for culture. The

commonly accepted assumption that cultural changes are more rapid than genetic ones should be tempered, because the more socially constrained the dissemination of the cultural variant, the more slowly changes will occur. This may explain the slow dissemination of behavior variants such as potato washing in Japanese macaques. Similarly, many traditional human societies prize cultural continuity, and changes in them take place only rather rarely.

Homogeneity of a culture is expected only under particular combinations of social norms and social models; it is not the rule. The more rigid the social constraints, the more homogeneous the cultural system of a population. We might expect social pressure to be greater in small and highly structured societies than in very large and loosely organized ones. Egalitarian societies will generally be less rigid, as in chimpanzees and some human hunter-gatherers, and probably less homogeneous. At the same time, in a huge modern Western society many cultural variants can survive side by side in most domains. Homogeneity is expected mainly in average-sized populations with considerable imposition.

Social norms reduce the diversity of cultural variants within the group, and social models increase the clustering of variants. Here, we face the "cultural paradox": culture requires sociality with social learning, but this very sociality may hinder cultural evolution. It is obvious from table 2 that one answer to this paradox is found in social structure. It is social structure that imposes social constraints on cultural change, and thus an understanding of the dynamics of cultural evolution requires an understanding of social change. Socially, cultural innovations are not all equal. When the innovators are members of an imposing group or prestigious, group members are prepared to learn from them, and cultural changes may be very rapid. If the same innovation is introduced by youngsters or members of the group without influence, it is likely that the innovation will rapidly disappear. Many examples of innovation in chimpanzees have been observed (Boesch 1995, Nishida 1987, Kummer and Goodall 1985), and most of them have disappeared rapidly. Therefore, some group members are "cultural facilitators." If they innovate, the variants spread rapidly; if others do, they indirectly block dissemination. Under this scheme, the adaptive value of the cultural variants is irrelevant. One class of cultural facilitators needs to be mentioned, and this is teachers: if teaching is being used under the family or the prestige model, then dissemination of a variant may be very rapid. Thus, teaching is a powerful tool for promoting cultural evolution.

Dissemination can be accomplished between individuals of the same generation (horizontal transfer), between individuals of different generations but within a genealogy (vertical transfer), or between genealogical lines (oblique transfer) (Cavalli-Sforza and Feldman 1973). For example, in the family model dissemination will be mainly vertical, and in the prestige and association models it will be mainly horizontal or oblique. One important addition, here, is that dissemination may be

TABLE 2
*Effects of Social Constraints
on Cultural Dissemination*

Social Model	Social Norm		
	Free Choice	Convention	Imposition
Individual	Many, rapid	Some, medium	Few, medium
Family	Variable, ^a medium	Few, slow	One, slow/medium
Association	Variable ^b medium	Few, slow	Few, slow/medium
Majority	One, slow	One, slow	One, slow
Prestige	Few, slow/rapid	Few, slow/rapid	One, slow/rapid

NOTE: Entries are number of clusters of cultural variants expected and rate of possible cultural change. Multiple rates reflect influence of individual innovators (e.g., change will be slow unless a prestigious individual introduces the variant).

^aA direct function of the number of family members present in the population.

^bA direct function of the social clustering within the population.

direct or indirect. When direct, there is perceptual contact between the model and the chooser; transmission takes place within a single group and between generations living at the same time. When indirect, transmission can be effected between individuals who are not in perceptual contact. Obviously, the acquisition mechanism can operate only if the information is made available to naive individuals in the absence of the model, and this is possible only if the information can be stored in an abstract form (Heyes 1994). This mode allows cultural change on a larger scale by facilitating transmission over much greater time and space ranges. It is typical of modern human societies and seems to be exclusive to them, indicating that language may make for a qualitative difference and that human cultures based on this type of transmission may be capable of much more rapid evolution.

Using different reference groups may provide different benefits, and one obvious one is that it makes it easier to evaluate options. Young group members have much to learn during the socialization process, and relying on different reference groups is one way to make a choice without having to evaluate all the alternatives through long and elaborate testing, especially when they involve aspects the benefits of which cannot be directly ascertained. This process may in the end cause some individuals to adopt less efficient solutions, but the time gained in selecting options may compensate for this. An alternative is that the differences in benefits between options may be too small to warrant elaborate selection procedures (Dawkins 1976, Durham 1991).

In conclusion, social constraints can dramatically affect cultural dissemination and cultural changes in various ways. Two important predictions may be advanced. First, the stronger the social constraints, the less rapid the dissemination of cultural variants. This can in the extreme prevent the introduction of a new cultural variant into a population. Second, cultural homogeneity will be expected in only a relatively few rigidly controlled populations; otherwise, cultural systems will be quite heterogeneous not only within a single population but sometimes even for a single cultural domain within that population.

Mechanisms of Social Learning

In addition to the question of which individuals in a population are exposed to and engage in a particular behavioral practice, there is the question of how those individuals acquire that practice. This is an important question in the current context because behavioral traditions whose origin and maintenance depend on different acquisition mechanisms may have very different properties with regard to their stability in the face of changing ecological or social conditions. The term "social learning," as it is typically used by psychologists, refers to situations in which one individual comes to behave similarly to others (thus, one animal's learning

things about others in its group, e.g., about dominance relations, is not social learning in this sense). There are a number of different ways in which individuals in a group may come to behave similarly (Whiten and Ham 1992) and these various processes may be explicated most clearly by distinguishing the learning of instrumental behaviors such as tool use from that of social behaviors such as gestural communication.

INSTRUMENTAL BEHAVIOR

Perhaps the simplest social learning process in instrumental situations is *local enhancement* (Thorpe 1956) or stimulus enhancement (Spence 1937). Local enhancement is widespread in the animal kingdom and refers to situations in which animals are attracted to the locations at which conspecifics are behaving (or perhaps to stimuli with which they are interacting). This then places them in a position to learn something that they would not otherwise have learned, and what they learn is often identical to what their conspecifics are learning. Nothing is actually learned from the behavior of others.

Animals may, however, sometimes learn things about the environment by observing the manipulations of others. For example, by observing others one individual may learn that a nut can be cracked and food found inside, a log can be rolled over and food found under it, sand comes off food when it is in water, and a piece of fruit hit with a stick may fall to the ground. In the terminology of Gibson (1979), by observing the manipulations of other animals individuals may learn "affordances" of the environment that they would be unlikely to discover on their own. The process whereby an individual observes and learns some dynamic affordances of the inanimate world as a result of the behavior of other animals and then uses what it has learned to devise its own behavioral strategies is called *emulation learning* (Tomasello 1990, 1996).

Despite the power of local enhancement and emulation learning to help individuals benefit from the knowledge and skills of others, these processes operate without the individual's paying attention to the behavior of other individuals at all. In some circumstances, in contrast, individuals seek to reproduce the behavior of others, presumably by noting some potential correspondence between it and their own behavior. How this is done varies as a function of the way in which the individual understands the behavior of others. For example, the mimicking of human speech by some birds is behavioral reproduction that would seem to take place on the perceptual or sensory-motor level only, since the birds do not seem to understand the human purpose of these sounds—at least not in the way that children learn linguistic symbols for conventional communicative purposes. Tomasello, Kruger, and Ratner (1993) have argued that humans perceive and understand the behavior of others in intentional terms—they see another's behavior as "cleaning the window" rather than as "moving her hand in a circular motion on the surface

of the window while holding a cloth"—and so when they seek to reproduce a behavior only certain aspects of the behavior appear relevant; for example, they may not consider which hand is used or how many times the surface is wiped. This is the archetype of *imitative learning*, at least in its human form: reproduction of both the behavior and its intended result.

In general, experimental studies with captive chimpanzees have found little evidence of the imitative learning of instrumental behaviors. For example, Tomasello et al. (1987) trained an adult chimpanzee demonstrator to rake food items into her cage with a metal T-bar, in some cases in very distinctive ways. Young chimpanzees that observed these behaviors learned more quickly than a control group, demonstrating some effect of their observations. However, they mostly used their own strategies to rake in the food, and not a single individual copied the distinctive techniques used by the demonstrator when the food was in an especially difficult location. Similar results were obtained by Nagell, Olguin, and Tomasello (1993), who gave chimpanzees and children a tool that could be used in either of two ways with the same end result. Some subjects observed a (human) demonstration of one method of tool use and other subjects observed a demonstration of the other, more efficient method. Whereas children in general copied the method of the demonstrator, whichever it was (imitative learning), chimpanzees used the same method or methods no matter which demonstration they observed (emulation learning). In a recent experiment with a similar logic, Whiten et al. (1996) found some evidence that chimpanzees could copy human behavior in opening a box containing food. For example, chimpanzees that saw a human push a stick through a lock, allowing the box to be opened, performed this behavior quite often, whereas chimpanzees that saw a human pull the stick out (with a twisting motion) performed that behavior. However, Tomasello (1996) has suggested that emulation learning may also have been at work in this case, as the human manipulations in all cases served to reveal distinctive affordances of the foraging box.

Interestingly, it is chimpanzees raised in human-like ways that provide the clearest evidence of imitative learning in instrumental contexts. For example, Tomasello, Savage-Rumbaugh, and Kruger (1993) studied the social learning of mother-reared captive chimpanzees and bonobos, enculturated chimpanzees and bonobos (raised in human-like cultural environments), and two-year-old children. Each subject was shown 24 different and novel actions on objects and encouraged to reproduce them: children were told to "do this," and the apes were pretrained to reproduce the modeled actions. The major result was that the mother-reared apes hardly ever engaged in imitative learning in which they reproduced both the end and the means of the novel actions, while the enculturated apes and the children imitatively learned the novel actions much more frequently (and equally).

The behavioral traditions of chimpanzees in the wild may be supported by either emulation learning or imitative learning. The wild behavior that has been documented in most detail is clearly nut cracking. As shown previously, this is a behavior whose geographical distribution in West Africa is almost certainly not explainable in ecological terms. Which of the two social learning processes is responsible for the cultural transmission is unknown, and therefore we shall discuss both. If a single chimpanzee in West Africa had invented nut cracking, its behavior would have left a stone hammer, some uncracked nuts, and some cracked nuts all in one place near a suitable substrate—very propitious learning conditions that might have facilitated the individual learning of others. Moreover, observation of its behavior would have demonstrated various affordances of nuts and stones. Thus, the combination of propitious learning conditions and processes of local enhancement and emulation learning might have resulted in the acquisition of nut cracking by the inventor's groupmates. This hypothesis is supported by the research of Sumita, Kitahara-Frisch, and Norikoshi (1985), who looked very closely at the acquisition of nut cracking by individual chimpanzees in a captive group setting and found that acquisition was very slow and gradual for all individuals and highly idiosyncratic. They concluded that individual trial-and-error learning (along with local enhancement) was responsible for the spread of the behavior in the group. At the same time, the imitative-learning hypothesis for nut cracking has intriguing support. Boesch (1996a, b) compared the nut cracking of a captive group of chimpanzees with that of the Taï chimpanzees in the wild in terms of the specific behavioral strategies used. What he found was that of the 14 strategies used by the captive group (e.g., hitting the nut with a hand, shaking it, stabbing it with a stick, throwing it against a hard surface), only 6 have been observed in Taï chimpanzees (and these employed one strategy not observed in the captive group). The argument was that the behavior of the Taï chimpanzees had become socially "canalized" into certain strategies even though the desired end result of cracking the nut was obviously the same in both groups—suggesting the possibility of imitative learning.

The other example outlined in detail above concerns ant dipping, in which many adult Gombe chimpanzees have been observed to use one technique and almost all adult Taï chimpanzees another. Such group differences in method of accomplishing the same goal are clearly suggestive of imitative learning. One argument against such an explanation is the possibility that what is being observed is individual rather than group differences. However, the large number of adults in both populations consistently using their group-specific method of dipping for ants makes this a very good candidate for a cultural behavior transmitted by means of imitative learning—to the degree that we can rule out possible ecological differences between the two locales in terms of such things as the living conditions and behavior of

the ants being caught and eaten. Boesch's personal testing (1990, 1996a, b) of the two group-specific techniques on driver ants at the two sites has suggested that the ecological conditions prevailing at those sites cannot explain the observed differences.

Overall, then, chimpanzee social learning of instrumental behaviors clearly involves processes of emulation learning that are almost certainly an important force in human cultural transmission as well in such things as tool use. Imitative learning has been demonstrated in some captive chimpanzees and is a viable explanation for nut cracking and ant dipping in wild chimpanzees. Why not all chimpanzees exhibit this ability and how frequently imitative learning takes place in wild chimpanzees remain very open questions at this point. Most of these experiments have been done with captive animals, whose lives are in many ways less cognitively and socially complex than those of their wild conspecifics, and, indeed, studies with animals raised and enculturated like children seem to show more persuasive skills in imitative learning. Thus the issue becomes whether the enculturated chimpanzees are simply experiencing some of the complexities that wild chimpanzees experience and so are more representative of life in the wild or whether human training has given them some species-atypical skills and abilities and it is the captive animals that are the more representative.

A further issue, assuming that an individual is capable of imitative learning, is under what conditions this individual will learn a task through emulation or through imitative learning. One possible answer is that imitative learning requires a "good" model. Individuals will imitate only if they have acceptable family, association, or prestige models; otherwise they will prefer to conduct detailed tests of alternatives to avoid failure. Orangutans have been shown to learn only from certain special social partners (Russon and Galdikas 1995). Chimpanzees in the wild and those enculturated like children will have such good models; captive chimpanzees mostly do not. Another possibility is that an individual learns imitatively when it pays to do so and will not do so for all tasks. This raises the question under what conditions imitation is better than emulation or local enhancement. Humans do not learn everything by imitation despite possessing the ability, and this may also be true of other animal species. One explanation is that in tasks that require a certain amount of individual evaluation of results it is better not to imitate.

COMMUNICATIVE BEHAVIOR

Communicative behavior presents a slightly different set of issues for questions of social learning. The main issue is that many communicative behaviors may be learned by a process called *ontogenetic ritualization* that is simply not available in the instrumental domain because it depends on the interaction of two individuals. In ontogenetic ritualization a communicatory signal is created by two individuals shaping one another's

behavior in repeated instances of a social interaction. For example, a juvenile may initiate play with a peer without warning simply by jumping on him to wrestle, slapping him on the head as she does so. The recipient may notice that such initiations always begin with the initiator's raising her arm in preparation for slapping and so anticipate by responding to that "intention movement" alone (Tinbergen 1951). The initiator notices the recipient's anticipation and understands that the "intention movement" by itself is sufficient to initiate the play and so in some future encounter raises her arm to initiate play. A slight variation on this process occurs with a special class of chimpanzee signals that have been called "attention-getters." These consist of behaviors such as slapping the ground that make a noise so that others look at the signaler—who may be displaying a play face or an aggressive or sexual posture to which the signal serves to draw attention. This is ontogenetic ritualization of a spontaneously produced behavior rather than an intention movement, but the process is essentially the same.

The point is that in both of these forms of ontogenetic ritualization, two individuals essentially shape one another's behavior over time. It is not the case that one individual is seeking to imitate the behavior of another, and so this is not imitative learning. There is no question that ontogenetic ritualization plays a very important role in the genesis of many chimpanzee gestural signals and very likely many human gestures (Tomasello and Camaioni 1997). The question, then, is whether imitative learning plays some role as well. The most systematic investigation of this question is by Tomasello and colleagues, observing a colony of captive chimpanzees (Tomasello, Call, et al. 1994, Tomasello, George, et al. 1985, Tomasello, Gust, and Frost 1989). The main result for current purposes is that there is little or no evidence for imitative learning in the communicative gestures of these chimpanzees. First, these captive individuals produce a number of idiosyncratic signals (Goodall 1986 also reports this for the Kasakela community at Gombe). Second, many youngsters also produce signals that they have never had directed to them (for example, others have never begged food or solicited tickling or nursing from them). Third, longitudinal observations have revealed considerable individuality in the use of gestures and individual variability both within and across generations. Finally, in an experimental investigation it was found that when an individual was removed from the group and taught an arbitrary signal (by means of which it obtained desired food from a human) observing individuals never reproduced that signal.

There are two sets of studies relevant to the social learning skills of enculturated chimpanzees in the domain of communication. As in the case of instrumental behaviors, they show that at least some chimpanzees with the appropriate kinds of experience can learn to imitate novel behaviors. The first set of studies, dealing with the process by which apes learn human-like com-

municative symbols, initially indicated that for apes learning a manual sign language by far the most effective technique was a molding of the hands and that imitation was a poor way to teach the animals signs (Fouts 1972). Since then Savage-Rumbaugh et al. (1986) have reported that the bonobo Kanzi acquired all of his earliest communicative symbols via imitative learning, in this case by manually contacting the lexigrams on a keyboard (although the documentation for this was very informal). The same basic finding also applies to a common chimpanzee raised and trained in much the same way (Savage-Rumbaugh et al. 1993). The movements involved here are quite simple (touching a particular place on a keyboard), but the communicative functions reproduced—the referential situations appropriate for different signs—may be quite complex. The second set of studies has examined the copying of movements specifically. Hayes and Hayes (1952) trained their human-raised chimpanzee Viki to mimic various body movements and gestures, for example, blinking the eyes or clapping the hands, over a seven-month period. In general, she reproduced them faithfully over time; she had clearly “gotten the idea” of the mimicking game. Cusance, Whiten, and Bard (1996) have more rigorously demonstrated similar abilities in two nursery-reared chimpanzees that had been trained for several months much as Viki had been.

In the wild, one communicative gesture, leaf clipping, has been claimed to be culturally transmitted or learned by means of imitative learning. Initially thought to be unique to the Mahale K group (Nishida 1980), it was later observed by Sugiyama (1981) in another group across the continent and by Boesch (1995) in the Tai group. The general point is that leaf clipping has been observed in several groups that have not had the opportunity to observe one another. Either the behavior has been spontaneously invented in all these groups by some kind of ritualization process, perhaps with some within-group emulation learning as individuals discover the affordances of the leaf for noise making by observing others rip up leaves, or it has been imitatively learned from an inventor. Leaf clipping as an attention-getter would have a very general communicative function; its immediate effect is that others look at the noise maker, who may be engaged in some other communicative display (for example, expressing a mood). There is thus much room for individual learning of the more specific communicative functions. However, at Tai, as we have seen, leaf clipping was used systematically for ten years by adult males not in an attention-getting situation but mostly when alone and warming up for the drumming sequence near a large buttress tree, and therefore Boesch's (1995) recent observations on the change in function of leaf clipping for many Tai chimpanzees are intriguing and await an explanation.

In line with the social learning of instrumental behaviors, then, the learning of communicative gestures and signals by wild chimpanzees involves emulation learning, ontogenetic ritualization, and probably imita-

tive learning. Captive chimpanzees provide very little evidence that an individual can observe another individual signaling for a communicative purpose and then, when it has the “same” communicative purpose, produce the same gestural signal. Chimpanzees raised and trained by humans in something like human sign language may learn some of their signals by means of imitative learning, which is clearly the case for arbitrary body movements. Many months of fairly intensive training are required for this skill to show itself, however, and the question is therefore whether it is a case of humans providing chimpanzees with the kind of rich environments and motivations that more closely resemble the wild situation or whether, on the contrary, we are witnessing a case of animals being trained to do human-like things that they would not do if left to their own devices.

The comparison with humans in the domain of communication involves language acquisition, of course. Linguistic symbols can only be learned via imitative learning, since there is virtually no way to discover arbitrary social conventions on one's own. Similar to human-raised chimpanzees, children do not start to learn linguistic symbols very rapidly. It is only after many months of social interaction in a symbol-rich environment that children start to learn a few words. After some years, children in all cultures acquire much of their communicative repertoire through imitative learning. In terms of frequency, by even the most conservative estimates this would involve the learning by children in all cultures of several new linguistic symbols per day for a period of some years (Carey 1982). Language and possibly some cultural conventions are clearly learned through imitative learning in humans.

TEACHING

If teaching is defined very broadly to include any behavior of one animal that serves to assist another animal's learning, teaching is relatively common in the animal kingdom (Caro and Hauser 1992). But flexible and insightful forms of instruction in which one individual intends that another acquire a skill or piece of knowledge and adjusts its behavior contingent on the learner's progress in skill or knowledge would seem to be very rare. Adopting this intentional definition of teaching, Boesch (1991) observed a number of instances of teaching among Tai chimpanzees in the context of nut cracking. He divided his observations into “facilitation” and “active teaching.” Observations of facilitation were fairly common and included such things as mothers' leaving intact nuts for their infants to crack (which they never did for other individuals) or placing hammers and nuts in the right position near the anvil for their infants to use. Active teaching was observed in only two instances, one in which a mother slowed down and modified her nut cracking and one in which a mother modified her son's positioning of the nut—in both cases as adjustments to the difficulties their offspring were hav-

ing with the procedure. These instances of active teaching are very important because they seem to be of the type characteristic of all human cultures as they instruct their youngsters in at least some important cultural activities (Kruger and Tomasello 1996). This kind of instruction may be seen as a very powerful facilitator of social learning, since carefully crafted demonstrations would seem to frame and support developing youngsters' attempts at imitative learning. Facilitation would also seem to be important, as it exposes youngsters to novel learning experiences, but in this case the learning is left up to them.

Cultural Change and Evolution

It is clear from all of the foregoing that chimpanzees learn from one another socially and thus transmit information culturally. How they do so is important not only in its own right but also for attempts to determine whether there are different kinds of cultural change and evolution for different cultural traditions or for different species. Specifically, it may be important for distinguishing chimpanzee culture and its evolution from human cultural evolution.

Cultural evolution refers to a number of processes by which a cultural tradition—multiple individuals in a group performing the same socially learned behavior for the same function—within a population may change over time. For example, a particular tradition may simply die out; this may happen if the environmental function somehow disappears (e.g., an insect prey disappears from the local environment) or if the social structure of the group somehow changes so that youngsters no longer come into contact with the appropriate social models (e.g., are suddenly not allowed to go with adult males to hunt). Alternatively, if it serves its functions adequately and the relevant environmental conditions remain constant, a cultural tradition may persist over a long period of time. Beyond simply dying out or staying the same, moreover, some cultural traditions change over time in ways that seem to be adaptive. One way might be termed "drift"; for example, an insect prey may change its habitat, thus leading the group to adapt to the changed conditions through individual and social learning. Another might be termed "branching," with a single cultural tradition spawning variants for different situations, for example, as leaf clipping by the Tai chimpanzees, originally used only in the drumming context, began being used in the resting context as well and as leaf grooming in Gombe chimpanzees has branched from an unclear function to include ectoparasite squashing (Boesch 1995). The branching process might be supposed to allow for more rapid diversification, as it would seem to require less in the way of innovation than the creation of totally new cultural behaviors.

Finally, there is another kind of evolutionary change that may or may not be characteristic of chimpanzee cultural traditions, and that is the type displayed by

many (but by no means all) human cultural traditions. Many human cultural traditions show an accumulation of modifications over generations in the direction of greater complexity, in such a way that a wider range of functions is encompassed. This may be called cumulative cultural evolution or the ratchet effect (by analogy with the device that keeps things in place while the user prepares to advance them further). For example, the way in which human beings have sheltered themselves has evolved significantly over human history as individuals in particular cultures have adapted their existing shelters to shield them from various aspects of the weather (e.g., rain, cold, sun) and various types of predators and pests, to provide themselves with privacy and protection from groupmates, and so on. Although we do not have such detailed artifactual records, it is presumably the case that some cultural rituals and conventions (e.g., human languages and religious rituals) have become more complex over time and been modified to meet novel communicative and social needs. This process may be more characteristic of some human cultures and some behavioral practices than of others, but all human societies would seem to have at least some artifacts produced by the ratchet effect (at the very least language and a few tools).

The problem in the case of chimpanzees is that we have not observed them in their natural habitats for long enough to know whether some of their practices show the ratchet effect; 30 years is simply not enough time. Moreover, the foregoing analysis of social constraints on the dissemination of cultural variants among chimpanzees suggests that any cumulative cultural evolution may be limited to a small subset within a population or a few selected traditions. It may even be that in chimpanzee society new cultural variants are actively discouraged in many domains, the way they are for some domains of activity in some human cultures. We do not know, then, to what extent some chimpanzee cultural traditions may show cumulative cultural evolution of the type that seems to make many human artifacts so useful and powerful both cognitively and socially.

It seems possible, however, that chimpanzee cultures do not evidence cumulative cultural traditions to the same extent as human cultures. Two aspects of the transmission landscape of chimpanzee cultures may limit the effectiveness of the ratchet effect; "slippage" in the transmission of information can limit both the range and the precision of this effect, and inconsistent transmission can block it altogether. With regard to the first, local enhancement, emulation learning, and ontogenetic ritualization allow for too much slippage or noise in the transmission process to produce good ratchets. Thus, if one individual chimpanzee invented a more efficient way of ant dipping that applied to a wider variety of ant species (e.g., by moving the stick in a particular way that led more ants to crawl onto it), youngsters capable only of emulation learning would not reproduce this precise variation because they would not

focus on the innovator's behavioral techniques. Youngsters that were capable of imitative learning (and judged that the innovation was "better" than their current practice) would adopt the new behavioral technique with very little slippage, and this might then set the stage for further innovations that built upon one another across generations. This same process would seem to be at work in the case of social behaviors such as communicative gestures as well, with cumulative cultural evolution occurring only if youngsters copy conspecifics relatively faithfully over time. Slippage strongly limits the precision and range of information acquired through the ratchet effect. It may be that it is teaching that best limits slippage and only once teaching is regularly used will the ratchet effect work effectively. Tomasello, Kruger, and Ratner (1993) have hypothesized that chimpanzee cultural traditions and artifacts do not show the ratchet effect because chimpanzees do not often imitate the instrumental actions of conspecifics or engage in intentional teaching. It is a paradox that cumulative cultural evolution depends on two processes, innovation and imitative learning (perhaps assisted by active teaching), one of which is typically an individual enterprise and the other of which excludes individual testing. Cumulative cultural evolution implies a combination of individual evaluation of the cultural variants present in a population and faithful imitation of the variant that has been judged to be the "best." Thus, whereas chimpanzees are quite adept at individual cognition and even cultural innovation (Boesch 1995, Kummer and Goodall 1965), they may not be so adept at the imitative learning and active teaching that serve to pass along these innovations to others; the evidence, as cited above, is incomplete.

The second possibility is that inconsistent transmission may block cumulative cultural evolution. Not all individuals of a species may be able to imitate, or some individuals may not imitate all possible models. This may have as an effect that new cumulative changes will only irregularly or rarely be transmitted, thereby blocking the ratchet effect. Boyd and Richerson (1996) have speculated in a paper entitled "Why Culture Is Common and Cultural Evolution Is Rare" that imitation and teaching, the psychological supports for cumulative cultural evolution, may be rarer in individuals of other species than they are in humans. If only some individuals imitate and teach and/or do so only rarely, cumulative cultural evolution will be quite difficult, as there will be many weak links in the chain of transmission. The argument is thus that the difference between human and chimpanzee cultural transmission mechanisms is not qualitative but only a quantitative difference in the frequency and prevalence of imitation and teaching, which may lead to qualitative differences in the types of cultural evolution that may occur. This hypothesis would account for the fact that in some chimpanzee populations and for some tasks imitative and teaching abilities are most likely present but no evidence of cumulative evolution has yet been gathered.

The problem with testing our two hypotheses is simply that at the moment there are no data that would allow us to quantify the frequency of imitative learning events in either chimpanzee or human societies.

The question of cultural evolution is a vitally important one. Understanding the differences between cultural evolution processes in chimpanzees and in humans will help us to identify what is unique about the artifacts and practices of the two species and what makes them such powerful facilitators of individual cognition and practice (Tomasello and Call 1997). Children inherit from their forebears not just their genes but their environments, full of cultural products (including language) with long histories of invention, use, and modification, and "all" they have to do is imitatively learn from others how to participate in the requisite practices. Whether chimpanzees have the social cognitive skills to create and participate in artifacts and practices in this way is unknown at this time. We have suggested two hypotheses for the possible absence of the ratchet effect in chimpanzees. In addition, we need to consider the possibility that chimpanzees may live in a social and physical environment in which elaborate cultural artifacts resulting from the ratchet effect are rarely needed.

Conclusion

Ideally, with enough information, we should be able to construct for specific populations of both humans and chimpanzees a kind of catalogue of "cultural phenotypes." In this catalogue, a specific tradition in a specific population would be described both in terms of the social norms/models that determine its social distribution and in terms of the social learning mechanisms that support the tradition and its patterns of change over time. We are currently very far from this ideal, mostly because of a lack of basic descriptive information on specific cultural traditions and how they work in specific populations of both humans and chimpanzees.

In the meantime, the central theoretical point in all of the foregoing—a point that we believe should guide future research efforts—is that culture is not a thing but a set of processes. These processes show much diversity both in the social norms and models that determine which individuals will be exposed to particular cultural variants and in the social learning mechanisms that determine the fidelity of transmission of the variants over time. Recognition of the diversity of social norms and models is important because it means that we must look for cultural outcomes not just at the population level but also in various subpopulations and identify the social norms that constrain their dissemination. Recognition of the diversity of social learning mechanisms is important because manner of transmission is an important determinant of patterns of cultural change and evolution.

In comparing chimpanzee and human cultures, we have noted many deep similarities. Both chimpanzees and humans have patterns of activities that are socially learned and that persist across generations, helping youngsters to adapt to their environments in ways that presumably are more efficient and less costly to learn than any techniques they might discover for themselves. However, we have also pointed briefly to one possible difference involving the use of indirect means of transmission, language, that may allow humans to transmit information over greater stretches of time and space and perhaps even to transmit different kinds of information. We also have indicated another possible difference involving cumulative cultural evolution as produced by the ratchet effect (which was probably necessary for the evolution of modern languages). Some human cultural traditions and artifacts seem to accumulate modifications over time so that their range of usefulness is gradually widened. This process depends on individuals' imitating the behavioral strategies of others and possibly on active instruction at a certain rate. Whether chimpanzees have some traditions of this type is unknown because we have not been observing them for long enough to know. This is therefore a very important question for future research. If it turns out that what distinguishes human culture is both language and cumulative cultural traditions depending on imitation and teaching, it is plausible to look for a common explanation in the way in which human beings understand one another as intentional and mental agents, since this understanding allows them both to learn from and to communicate with others in new and powerful ways (Tomasello, Kruger, and Ratner 1993).

Before we come to such a conclusion, however, we must obtain more descriptive information on chimpanzee and human populations in their natural habitats, and we must conduct more focused studies as well. Some of the questions most in need of answers are the following: (1) What are the relative rates of imitation and instruction (as well as innovation) in human and chimpanzee populations? (2) What is the role of social constraints in human and chimpanzee cultures? (3) Are there chimpanzee cultural traditions that we have not seen because they are confined to subgroups within populations (e.g., families)? (4) Is there cumulative cultural evolution in some chimpanzee traditions that we cannot see because we have not been observing for long enough or perhaps not observing in the appropriate ways? (5) Is the reason that chimpanzees do not imitatively learn very well in captivity without human instruction that they have grown up in impoverished conditions or that they need human instruction to acquire this skill? (6) Is the reason that human-raised chimpanzees imitate more readily that they have lived in captive conditions more like their own rich social lives in the wild or that they need human instruction to acquire this skill?

It is clear that the processes that make up the human cultural tree have very deep evolutionary roots, and we

cannot hope to understand the branches and leaves of this tree without an understanding of these roots. In performing comparative studies with chimpanzees in particular, it is vitally important that we not become distracted by volatile issues of human uniqueness or lack of uniqueness but focus on both the similarities and the differences so that we may understand more deeply the working of culture as an evolutionary process.

Comments

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A key concept that emerges from Boesch and Tomasello's discussion is that of emulation learning. This is taken to be a probable ability of chimpanzees and used as the "kill-joy" alternative in attempts to discover imitation. I question whether emulation learning has been sufficiently well established to function as a null hypothesis in this way and whether its definition is precise enough for reliable identification of its operation.

Emulation is a slippery customer. Tomasello et al. (1987) suggested that when chimpanzees observed raking what was made more salient was the tool in its function as tool. Later, the word "emulation" was used for the situation in which a focus on the demonstrator's goal may lead the observer to be attracted to and seek to attain the goal and therefore attempt to reproduce it by whatever means it can devise (Tomasello 1990). This definition does not readily include learning an object's function as a tool, but Tomasello, Kruger, and Ratner (1993) clarify, describing emulation now as affordance learning: seeing a jar opened might allow the observer to recognize that the jar affords opening. Tomasello (1996:321) states that in emulation learning the learner observes and understands a change of state in the world produced by the manipulations of another, giving as examples the discoveries by observation that food may be located under logs, nuts can be cracked, and a stick's hitting a fruit will make it fall. By this point, emulation learning would seem to have departed a long way from Wood's (1989) original usage and to have become rather ambiguous. Among other possibilities, its meanings might include the following:

1. Setting a goal. Having seen the favourable result of another's actions, the observer tries to get the same reward in whatever way it can; the observed result has become a current goal. This phenomenon, if it exists, can be modelled as a simple priming effect (Byrne 1994, Byrne and Russon n.d).

2. Learning the physical properties of objects. Having

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