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 IN TUNE WITH OTHERS:
 THE SOCIAL SIDE OF PRIMATE CULTURE

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Imanishi (1952) . . . asserts that instinct is an inherited behavior and thus is something opposite to culture, which represents acquired behavior. If it is dogmatic to regard all animal behavior as instinctive, it is equally dogmatic to regard all human behavior as cultural, says Imanishi.

Itani and Nishimura 1973, p. 27

There is nothing more circular than saying that we, humans, are the product of culture if culture is at the same time the product of us. Natural selection has produced our species, including our cultural abilities, and hence these abilities fall squarely under biology. This inevitably raises the question whether natural selection may have produced similar abilities in more than one species.

That this controversial issue was first broached in the East rather than the West is not surprising, given how tightly the culture concept is interwoven with claims of human uniqueness. Plato's "great chain of being," which places humans above all other animals, is absent from Eastern belief systems, according to which all living things are spiritually connected (Asquith 1996; de Waal 2003a). As far back as 1952 Kinji Imanishi, a Japanese anthropologist, wrote an essay that challenged the human-animal divide. He inserted a fictional debate between a wasp, a monkey, an evolutionist, and a layman in which the possibility was raised that other animals might have culture. The proposed definition was straightforward: if individuals learn from one another, their behavior may, over time, become different from that in other groups, thus creating a characteristic culture.

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Figure 2.1 More than half a century after the sweet-potato-washing habit spread among Japanese macaques on Koshima Island, they are still doing it even though the current population has never known the innovator. Nowadays transmission is mostly from mother to offspring, although this was not so in the early years of the habit. The infant clinging to its mother may learn to associate sweet potatoes with the ocean simply by picking up dropped pieces. Photograph by Frans de Waal.

This approach brought culture down to its lowest common denominator: the social rather than genetic transmission of behavior. It was confirmed within a few years by observations of Japanese macaques (*Macaca fuscata*) washing sweet potatoes on Koshima Island (Figure 2.1). The thorough reports of Kawai (1965), Watanabe (1994), Hirata et al. (2001), and others show that sweet-potato washing spread among the monkeys in a manner consistent with the troop's social relationships. The first individuals to show the behavior after Imo, the juvenile female who initiated it, were her mother and age peers. Even though the Koshima study is a historic report that lacks controls, there are good reasons to consider it the first documented case of an innovation that became a tradition (de Waal 2001).

If animal groups vary with respect to a single behavior pattern, such as sweet-potato washing, there is perhaps no reason to employ the loaded "culture" label. "Group-specific behavior" or "tradition" will do. That things might not be so simple with regard to our closest relatives was first

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intimated by McGrew's (1992) review of tool use among wild chimpanzees. Since then a steady stream of new observations indicates an entire slew of cross-group variants in certain species, as amply evident in the present book. This justifies terminology that goes beyond mere "tradition." Our own definition of culture reflects this broader perspective:

Culture is a way of life shared by the members of one group but not necessarily with the members of other groups of the same species. It covers knowledge, habits, and skills, including underlying tendencies and preferences, derived from exposure to and learning from others . . . The way individuals learn from each other is secondary, but that they learn from each other is a requirement. Thus, the "culture" label does not apply to knowledge, habits, or skills that individuals can and will readily acquire on their own.

(de Waal 2001, p. 31).

The "culture" label thus befits any species in which one community can readily be distinguished from another on the basis of socially transmitted behavior (cf. Menzel 1973a; Bonner 1980). So far, there is good evidence for culture in many mammals, fish, and birds. Nevertheless, scientists trained in disciplines in which mechanisms are paramount, such as experimental psychology, sometimes resist the idea of animal culture by insisting on specific forms of social transmission—such as teaching and imitation—that most animals may not exhibit (e.g., Premack and Premack 1994; Tomasello 1994). They wonder if the learning mechanisms of humans and other animals are truly "homologous," that is, derived from common ancestry. Inasmuch as the fundamentals of learning, such as association and conditioning, are widespread, they are likely homologous. Beyond this, the homology concept is difficult or impossible to apply. This concept was developed for anatomical traits, which are easily defined and compared, and has been successfully extended to the muscle movements of facial expressions (Preuschoft and van Hooff 1995). But the question whether human and ape cognition are homologous will remain unanswerable until we have far more precise definitions and tests of the underlying capacities.

An alternative approach to culture, illustrated in the definition given earlier, considers learning mechanisms as secondary. This more evolutionary approach focuses on the effects and function of culture rather than the specific cognitive mechanisms that support it. In the same way that the definition of respiration does not specify whether the process takes place through lungs or gills, or the definition of locomotion does

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not specify whether it is accomplished with legs or wings, the concept of cultural propagation does not need to specify how organisms acquire behavior from each other.

As a result of these differing emphases, the debate about animal culture sometimes resembles one between two deaf men, with one insisting on acquired behavioral variants and the other on specific cognitive capacities. The present chapter explores mechanisms of cultural transmission, but not from the angle of cognitive complexity. We rather seek to explore the social nature of cultural learning, reviewing observations and experiments on brown capuchin monkeys (*Cebus apella*) and chimpanzees (*Pan troglodytes*). We believe that there is far more to social learning than simply individual learning in a social setting, as others have suggested. Social learning has unique dynamics of its own.

No Imitation without Identification

Three Theories of Social Learning

Japanese macaques have rubbed pebbles together for a quarter century on Arashiyama, a mountain that overlooks Kyoto. It is a peculiar behavior whose main feature is that it produces noise. The behavior is absent from nearby monkey troops. It is unknown exactly how the monkeys learn this so-called stone handling from each other: young monkeys must copy it from their mothers without ever being rewarded (Huffman 1996). The primate literature contains myriad examples of traditions of which the reinforcement is unclear (reviewed by de Waal 2001), which raises the possibility that primate social learning stems at least partly from conformism and a motivation to act like others.

To give this process a name and emphasize the role of social models, such as mothers and peers, we will use the acronym BIOL, which stands for Bonding- and Identification-based Observational Learning (de Waal 2001). Instead of being dependent on external reinforcement, BIOL is a form of learning born out of the desire to belong and fit in. Young individuals identify with certain models, which they copy in an often playful, imperfect, and exploratory fashion. These models act as “masters” to the naïve “apprentice” (Matsuzawa et al. 2001). Rewards are secondary, although one could argue that the copying of others is intrinsically rewarding.

This model conflicts with traditional learning theory. When Galef (1992, p. 171) claimed that “although imitation might introduce some

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novel behavior into the repertoire of members of a population, through time this behavioral novelty would be maintained, modified, or extinguished depending on its effectiveness in acquiring rewards,” he expressed the prevailing view that although social partners can influence behavior, learning is ultimately decided by tangible rewards. However, we know from mirror-neuron studies that monkeys do not need any rewards to match the observed actions of others to their own behavior; that is, mirror neurons respond similarly during an action performed by the monkey itself, such as grasping, and while watching another monkey perform a similar action. These “monkey see, monkey do” neurons do the same for entire chains of actions and their predicted outcomes. In other words, the *intentions* of others seem to be encoded from observed motor sequences. Thus social animals are hardwired to be in tune with each other at the level of both actions and goals (Fogassi et al. 2005; Fadiga and Craighero 2007).

Although these findings are usually discussed in the context of empathy, they bear on behavioral copying as well. In their simplest manifestations both mimicry and imitation depend on the degree to which the subject “maps” the model’s body movements onto its own (de Waal 2007). The predisposition to do so has high survival value in relation to group life. Primates are nomadic and hence need to sleep when others sleep, play when others play, and forage or hunt when others forage or hunt. Experiments show that satiated primates, like many other animals, begin eating again when they see others eat (Addessi and Visalberghi 2001; Ferrari et al. 2005; Dindo and de Waal 2007), scratch themselves when they see others scratch themselves (Nakayama 2004), and yawn in response to a video of a yawning conspecific (Anderson et al. 2004). This phenomenon is known as social facilitation. Novel behavior, too, is copied, at least by apes. Examples include the imitation of an unusual limping walk by juvenile groupmates of an injured adult male (de Waal 1982) and successful “do-as-I-do” experiments involving human models (Custance et al. 1995; Myowa-Yamakoshi and Matsuzawa 1999). A nice illustration of how unimportant tangible rewards are for this copying tendency comes from the nut-cracking attempts of young chimpanzees. During the first 5 years of their lives, they lack the strength and coordination to crack nuts with stones but continue to re-create the actions of their mothers without a single success (Matsuzawa et al. 2001).

De Waal (1998) proposed “identification” with others as the motivation behind behavioral copying. Like Preston and de Waal’s (2002)

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characterization of perception-action mechanisms for empathy, identification entails bodily mapping the self onto the other (or the other onto the self), resulting in shared representations with the other. This obviously requires a motivation to do so, in which motivation is thought to increase with social closeness and bodily similarity—such as with members of one’s own species and gender. It is hardly surprising, therefore, that after the initial skepticism about imitation in nonhuman primates, based on their failure to copy complex human actions (Tomasello, Kruger et al. 1993), two kinds of studies have yielded more promising results, namely, those concerning (a) human-raised apes watching a human model (Tomasello, Savage-Rumbaugh et al. 1993; Bjorklund et al. 2000) or (b) apes raised by their own kind watching a conspecific model (Whiten et al. 2005; Horner et al. 2006; Whiten this book). In both cases identification with the model species is facilitated by rearing history. It is also not surprising that when young chimpanzees learn to use a wand to fish for ants, daughters copy their mothers more faithfully than do sons (Lonsdorf et al. 2004). The tendency to copy another seems to vary with identification, therefore—a motivational issue not to be confused with cognitive capacity.

Table 2.1 compares the predictions of BIOL (i.e., social learning is guided by social relations, and extrinsic rewards are not essential) with predictions from traditional learning theory, according to which behavior will be extinguished in the absence of extrinsic rewards, as well as with predictions from vicarious learning theory (e.g., Bandura 1977), according to which seeing another individual achieve benefits will make observers attend to the model and aim for the same benefits.

Testing BIOL on Capuchin Monkeys

Brown capuchin monkeys are gregarious New World primates whose social structure is characterized by a loose dominance hierarchy and marked tolerance among unrelated individuals within the group. Although experimental evidence for social learning within the genus has been mixed, that individual behavior is influenced by others is certain. There are ample suggestions that behavior is socially transmitted in the field (Perry, Baker et al. 2003; Perry this book), and in an earlier experiment we found that these monkeys can learn which of two tokens yields the better reward from merely watching a partner exchange tokens for food (Brosnan and de Waal 2004). Capuchins thus provide an interesting model to address questions regarding social influences on learning.

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Table 2.1 Three theories about the role of reward in social learning

Theory	Who requires reward?		Prediction Effect(s) of tangible reward	References
	Model	Observer		
Vicarious reinforcement	Yes	No	<ul style="list-style-type: none"> • Attracts attention to model and facilitates acquisition by observer • Demonstrates adaptive (rewarding) value of modeled behavior 	Bandura (1977) Palameta and Lefebvre (1985) Akins and Zentall (1998)
Traditional learning	No	Yes	<ul style="list-style-type: none"> • Required to maintain a socially acquired behavior • Absence of reward leads to extinction 	Galef (1992) Galef et al. (1986) Heyes et al. (1993)
Bonding- and Identification-based Observational Learning (BIOL)	No	No	<ul style="list-style-type: none"> • Rewards not required • Emphasis is on social ties and attention to specific others 	de Waal (1998, 2001) Matsuzawa et al. (2001)

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Figure 2.2 A capuchin model opens one out of three boxes of different color and marking, while the test subject, behind mesh, stands upright to get a better look at the procedure. After this, the subject will be presented with a rearrangement of the same three boxes. Drawing from video still by Frans de Waal.

In order to study the role of food rewards in social learning, and more specifically to explore the competing predictions outlined in Table 2.1, we paired 13 adult capuchin monkeys with a familiar conspecific model, with each subject observing two or three models throughout the experiment, thus creating 34 unique model-subject pairs. Each pair was temporarily separated from its social group and brought into a mobile test chamber consisting of two equally sized areas separated by mesh. The monkeys could see and hear their partner but had no access to the other's space. We designed a simple test—three opaque boxes with hinged lids that were opened by the monkeys without training. Models were taught to open only one of the three boxes, and we were interested in whether the subjects, who were naïve to the contents of the box, would copy the models' choices (Figure 2.2).

On each trial the model was first presented with three boxes and allowed to open one. After the subjects observed this, the same three boxes were rearranged (forcing the subjects to attend to the color and pattern of the box rather than its relative position) and presented to the subject, who was allowed to make only one choice. Each test session consisted of 12 trials with the same boxes. We analyzed the proportion of trials in which subjects chose the same box as the model under the three following conditions:

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Neither Rewarded: All boxes were empty for both model and subject.

Model Rewarded: Only the model was rewarded for opening the trained box. The subject's boxes were empty.

Both Rewarded: The model was rewarded for opening the trained box, and so was the subject.

All subjects proceeded through each condition in this order, completing three sessions with each model before moving on to the next condition. We analyzed the data for the first two models observed by each subject and found that subjects copied the choice made by the model at a level significantly above 33.3 percent chance under all conditions: they did so on average in 44.6 percent, 46.1 percent, and 70.8 percent of trials in, respectively, the Neither Rewarded, Model Rewarded, and Both Rewarded conditions (Bonnie and de Waal 2007; Figure 2.3). Interestingly, we found no significant difference in performance between the Neither Rewarded and Model Rewarded conditions. Apparently, observing the model collect a reward does not enhance a capuchin monkey's inclination to copy the model, as predicted by vicarious reinforcement theory.

To see how often subjects would open a baited box by themselves, we added a Control condition in which a partner was present but not involved in the task. In these Control conditions the subject's random chance of finding a reward was the same as in the Both Rewarded condition, 33.3 percent, but subjects were significantly less successful at finding a reward in the Control than in the Both Rewarded condition, which suggests that model demonstrations did in fact enhance the subjects' performance.

These results support the BIOL model in that capuchin monkeys do not need to be rewarded, and do not in fact need to see another individual being rewarded, to copy the behavior of others. Even with no rewards in sight and no previous experience with baited boxes (as in the Neither Rewarded condition), there was still behavioral matching. Reinforcement also played a role, however. Monkeys chose the same box as the model significantly more in the Both Rewarded condition than in any other condition. Their performance increased noticeably, reaching around 90 percent correct on choices made in the final session.

A second prediction from the BIOL model is that a close social tie between two individuals will stimulate learning through observation (see also Coussi-Korbel and Fragaszy 1995). For each model-subject

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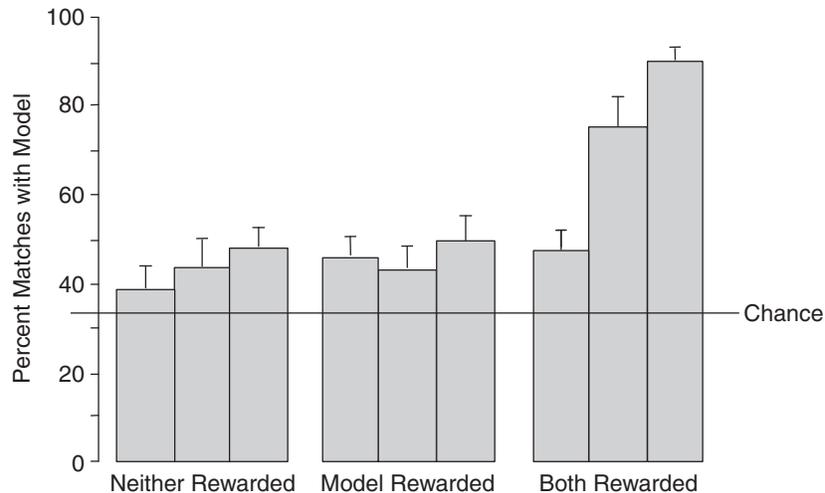


Figure 2.3 Mean (+ SEM) proportion of trials in which 13 capuchin monkeys copied the choices demonstrated by a conspecific model in the Neither Rewarded, Model Rewarded, and Both Rewarded conditions. All subjects were tested in that order in 12 trials per session and 3 sessions per condition. As can be seen, subjects were on average above the chance level of 33.3 percent even in the absence of any food rewards (as in the Neither Rewarded condition). Their performance improved dramatically when they themselves had a chance of gaining a reward. From Bonnie and de Waal (2007).

pair, we calculated a measure of affiliation, the Relationship Quality Index (RQI), used previously to qualify mother-infant relationships in our capuchin colony (Weaver and de Waal 2003). RQI is defined as the relative hourly rate of exchanged grooming and contact sitting (affiliation) divided by the relative hourly rate of agonistic exchanges and avoidance (aggression) occurring between two individuals. Relative affiliation and aggression rates for each pair were calculated by dividing the rate for each dyad by the average rate among all dyads in the group. We used behavioral data extracted from a 2-year database of regularly repeated 30-minute observations of the group, during which affiliative and aggressive behaviors were sampled while the monkeys were confined to the indoor area of their living quarters, free to associate with whomever they wanted. A dyad with a positive RQI has more observed instances of affiliation than of conflict and avoidance, whereas dyads

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with a negative RQI have a higher rate of conflict and avoidance than of affiliation.

For each subject, we categorized each model observed as having an RQI above or below the group median. We labeled these categories, respectively, AFF (predominantly affiliative) and AGG (predominantly aggressive and conflictual). Subjects for whom all models were of the same type were excluded from analysis. For the remaining subjects ($N=10$), we calculated the proportion of trials with either AFF or AGG models during which the subjects copied the model's choice. Doing so separately for each reward condition, we found that across all three sessions in the Model Rewarded condition, subjects copied the choices of AFF models 58.8 ± 18.5 percent (mean \pm standard deviation) of the time, which was significantly above the 45.0 ± 15.1 percent copying of AGG models (paired comparison with randomization test, $P=0.032$, two-tailed; Manly 1997). No such difference was found for the other two conditions ($P>0.10$).

Thus if rewards are available to the model only, subjects tend to match the model's choice, especially if they have a close tie with her. Possibly it is in these closer, more tolerant relationships that subjects follow the model's discoveries of food with the least inhibition. Competitive tendencies may interfere in the more distant relationships. If the model finds no food, on the other hand, tolerance versus competitiveness is not an issue, and hence the social relationship is less relevant. Similarly, when the subject has a chance to find its own food, the subject's competition with the model lessens because the baited boxes in front of the subject become the primary concern. These findings fit the BIOL model in that attention paid to others varies with previously established relationships; that is, competitiveness between two individuals interferes with social learning, whereas social tolerance promotes it (cf. van Schaik 2003).

Social Culture

Social Organization

Compared with variation in how primates deal with the environment (e.g., foraging for food, tool use), little attention has been paid to social culture, which we might define as the transmission of social positions, preferences, habits, and attitudes. This is a more elusive topic than material culture. In human culture, for instance, it is easy to tell if people eat

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with knife and fork or with chopsticks, but to notice if a culture is egalitarian or hierarchical, warm or distant, is much harder to capture in behavioral measures.

A well-documented primate example of social culture is the inheritance of rank positions in macaques and baboons. The future position in the hierarchy of a newborn female can be predicted with almost 100 percent certainty on the basis of her mother's rank. Despite its stability, the matrilineal system depends on learning. Early in life the young monkey finds out against which opponents she can expect help from her mother and sisters: she will end up dominating the parties she is supported against. Experiments that have manipulated the presence of family members have found that when support dwindles, dominant females are unable to maintain their positions (Chapais 1988). In other words, the kin-based hierarchy is maintained for generation after generation through social rather than genetic transmission.

The same applies to the affiliative network. De Waal (1996b) found that rhesus monkey (*M. mulatta*) daughters copy their mothers' association preferences. Even when they have grown fully independent and are approaching motherhood themselves, they spend much time with the daughters of their mothers' friends. We do not know exactly how friendships are being transmitted across the generations, but the simplest way would be that when two mothers sit down to groom and relax, their daughters take the opportunity to play nearby. Being playmates early on, these youngsters then develop an association for the rest of their lives. Given these processes, imagine that females in a particular group begin to strengthen ties outside their own families. Over time this trend will become more and more deeply embedded because their daughters will start doing the same; hence a different social culture will be born.

Cultural effects on social behavior have been documented in relation to conflict and conflict resolution. One experiment managed to turn monkeys into pacifists. Juveniles of two different macaque species were placed together, day and night, for 5 months. Rhesus monkeys, known as quarrelsome and violent, were housed with the more tolerant and easygoing stump-tailed macaques (*M. arctoides*). Stump-tailed monkeys easily reconcile with their opponents after fights by holding each others' hips, whereas reconciliations are rare among rhesus monkeys. Because the mixed-species groups were dominated by the stump-tailed monkeys, physical aggression was rare. The atmosphere was relaxed, and after a

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while juveniles of the two species played together, groomed together, and slept in large, mixed huddles. Most important, the rhesus monkeys developed peacemaking skills on a par with those of their more tolerant group-mates. The two species were separated at the end of the experiment, but even then the rhesus monkeys maintained a threefold higher reconciliation rate after fights with conspecifics than is typical of their species (de Waal and Johanowicz 1993).

Not unlike rhesus monkeys, baboons have a reputation of being fiercely competitive. Sapolsky and Share (2004) produced the first field evidence that these monkeys can deviate from this characterization. Wild olive baboons (*Papio anubis*) developed an exceptionally pacific social tradition that outlasted the individuals that established it. For years Sapolsky (1994) had documented how these baboons on the plains of the Masai Mara in Kenya wage wars of nerves, whereby the stress of conflict compromises their rivals' immune systems and increases the level of blood cortisol. An accident of history, however, selectively wiped out all the male bullies of his main study troop. As a result, the number of aggressive incidents dropped dramatically. This by itself was not very surprising. It became more interesting when it was discovered that the behavioral change was maintained for a decade. Baboon males migrate after puberty, and the study group had experienced a complete turnover of males during the intervening decade. Nevertheless, compared with neighboring troops, the affected troop upheld its reduced aggression, increased friendly behavior, and exceptionally low stress levels. The conclusion from this natural experiment is that like human societies, each animal society has its own ecological and behavioral history, which determines its prevalent social style.

Culturally Learned Communication

Expressions of emotions appear in every member of a species in similar or identical form even if opportunities for learning have been scant. As a parallel to deaf and blind children who, despite deprived learning opportunities, exhibit all human facial expressions in emotionally appropriate contexts (Eibl-Eibesfeldt 1989), a deaf female chimpanzee at the Arnhem Zoo seemed to utter all the varied calls of her species in the right context (de Waal 1982).

It is often assumed, therefore, that the production of communication signals is little affected by learning in primates (but see Tagliatela et al. 2003). The correct reading and interpretation of signals, on the other

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hand, seems open to environmental influences. For example, responsiveness to communication signals varies with exposure to species-typical stimuli and opportunities for associative learning (Mason 1985), and the appropriate response to alarm calls by juvenile primates increases with age and experience (Cheney and Seyfarth 1990).

To the general rule that the production of communication displays is less influenced by learning than their appraisal, one important exception exists, however. This is the culturally transmitted communication displays of the great apes, that is, displays that individuals learn from each other. The result of transmission through learning is that a group may develop a set of communication displays shared by all of its members yet distinct from the displays found in other groups. Thus most bonobos (*Pan paniscus*) in the San Diego Zoo show a ritual unknown in other bonobo groups, captive or wild. During grooming they customarily clap their hands or feet together or tap their chests with their hands. One bonobo will sit down in front of another, clap her hands a couple of times, and then start grooming the other's face, alternating this with more hand clapping. The behavior seems to function in the same way as the spluttering and tooth clacking of grooming chimpanzees, which express enthusiasm for the task. This makes the San Diego Zoo the only place in the world where one can actually hear apes groom. When new individuals are introduced, they pick up the habit in about 2 years (de Waal 1988).

Other examples of group-specific communication derive from a comparison of vocalizations across zoo groups of chimpanzees (Marshall et al. 1999), as well as from field studies on chimpanzees across Africa (Whiten et al. 1999). The latter report includes communication displays such as leaf clipping in courtship, the "rain dance," and handclasp grooming (discussed later). Recently, yet another custom was reported for wild chimpanzees, the so-called social scratch. In this gesture one individual rakes the hand back and forth across the body of another, usually scratching the other with the nails. It seems the typical "you scratch my back, I'll scratch yours" gesture, but however familiar this sounds, in wild chimpanzees the social scratch is limited to a single community (Nakamura et al. 2000). This behavior is thought to arouse pleasure in the recipient and to initiate a grooming session. In relation to the role of reinforcement, discussed earlier, it is intriguing that the main reward of this behavior goes to its recipient, as opposed to its performer.

Cultural communication patterns tend to be nonfacial and nonvocal, perhaps because of the apes' limited control over face and voice, espe-

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cially at emotionally charged moments. Also in humans, facial expressions seem less culturally variable than manual gestures. It is perhaps due to this bias that so few good examples of culturally transmitted communication exist for monkeys, because one of the striking differences between monkey and ape visual communication is the virtual absence of free-hand gestures in monkeys (de Waal 2003b). The observations of white-faced capuchin monkeys (*C. capucinus*) by Perry (this book) may constitute an exception in that they concern group-specific interaction patterns, not unlike the handclasp or hand-clap grooming described for apes.

Handclasp Grooming

In 1992 we first saw two chimpanzees at the Yerkes Primate Center's Field Station clasp their hands together while grooming (Figure 2.4). The two were sitting in a metal climbing structure grooming each other when one female, Georgia, unexpectedly took the hand of an older female and lifted both of their hands high into the air. They thus sat in a perfectly symmetrical A-frame posture, each with their free hand grooming the pit of the other's lifted arm. The great advantage was that the custom seemed to be in its early stages. Rather than encountering a wild community of chimpanzees that has been doing it for hundreds or perhaps thousands of years, here we had a group in which the behavior was initially extremely rare (only a dozen instances were seen in the entire first year of daily observation) and was always initiated by the same individual, Georgia, the presumed inventor. The posture strongly resembled the so-called handclasp grooming (HCG) reported for wild chimpanzees in the Mahale Mountains, Tanzania (McGrew and Tutin 1978).

A unique property of the handclasp grooming posture is that it is not required for grooming the armpit of another individual. Chimpanzees that do not perform HCG are no less hygienic in the underarm area than those who do. Thus it appears to yield no obvious benefits or rewards to the groomers. It has been proposed that handclasp grooming and even specific aspects of the posture itself act to symbolize a close relationship between the grooming pair. Indeed, the intimate nature of the posture involves a degree of cooperation and trust among the partners (McGrew and Tutin 1978; de Waal and Seres 1997). This has led to the hypothesis that the nature of the relationship between two individuals will predict the development of HCG between them. While we would

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Figure 2.4 One group of chimpanzees at the Yerkes Primate Center shows the handclasp grooming posture, also observed in a few wild communities. Here the posture is shown between the adult sister and the mother of the behavior's originator. Photograph by Frans de Waal.

expect to see HCG among kin or close affiliates, we would not expect HCG between two individuals who are rivals.

To explore this prediction, we analyzed retrospectively 11 years of data (from 1992 to 2003) on the occurrence of HCG in one group of chimpanzees at the Yerkes Field Station (a second group in identical surroundings at the same facility never showed the posture). During this period nearly 300 instances of HCG were observed by members of our team. The pattern spread gradually until all adults regularly performed HCGs (Figure 2.5).

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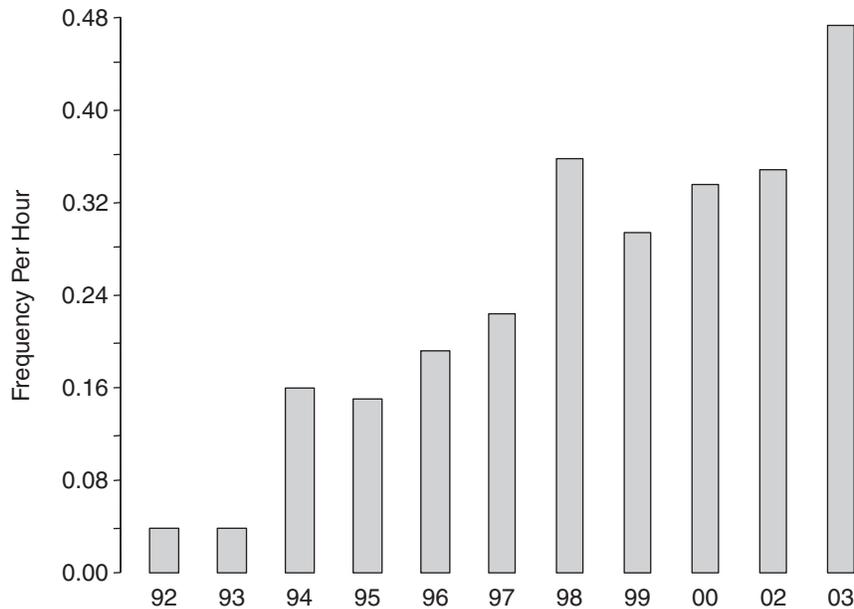


Figure 2.5 Rate per hour of observation of all handclasp grooming bouts from 1992 through 2003. The rate increased steadily and significantly throughout the study period. From Bonnie and de Waal (2006).

We were able to define for each year the degree of affiliation between all possible grooming pairs within the group. To do so, we looked at the proportion of scan samples collected during 90-minute observations of the group in its outdoor enclosure in which dyads were engaged in contact sitting, sitting within arms' reach, grooming, and mutual grooming. From these data a dyadic matrix was created of average proximity patterns (contact sitting and sitting within arm's reach). A second matrix included handclasp grooming, a binary variable regarding the occurrence or nonoccurrence of HCG within a dyad.

For each year the proximity matrix was correlated with the HCG matrix, and the results were compared with 5,000 random permutations of the same matrices (cf. Dow and de Waal 1989). Proximity was found to correlate positively with HCG, which confirmed our prediction that dyads with a higher rate of affiliative exchange were more likely to develop HCG than others. More than half of the top 25 percent of dyads in

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terms of affiliation were observed to engage in HCG. In contrast, of dyads that fell within the lowest quartile of affiliation, only 15 percent were observed to engage in HCG at some point during the study period. In addition, in nearly all dyads formed, at least one individual had been previously observed to handclasp groom. We concluded that affiliation and individual experience determine the spread of handclasp grooming (Bonnie and de Waal 2006).

Learning of Arbitrary Conventions

Social cultures, like material ones, require controlled experiments to explore how behaviors are transmitted within a group. Thus far, such experiments have included mimicking by apes of arbitrary gestures, body movements, and actions on objects that were demonstrated by humans (Tomasello, Savage-Rumbaugh et al. 1993; Custance et al. 1995; Myowa-Yamakoshi and Matsuzawa 1999; Call 2001) and the previously mentioned co-rearing of two different macaque species (de Waal and Johanowicz 1993). However, since all of these studies have relied on cross-species interaction, they have limited ecological relevance. No study has successfully generated a new social convention in an established group. Indeed, in a study in which one chimpanzee was trained to employ arm raising and other arbitrary gestures to gain food from a human, the behavior failed to be adopted by other members of its group (Tomasello et al. 1997). Even though this was a relatively short, single attempt, the authors took their negative finding to mean that nonhuman species lack the capacity to observationally learn the significance of arbitrary actions, a capacity considered fundamental to human culture.

Working with the same chimpanzees at the Yerkes Primate Center Field Station, we seeded in each of two groups a different endpoint to a complex action chain involving familiar objects. Although the chimpanzees were ultimately rewarded for completing the task, the study was not a tool task (as was Whiten et al. 2005), nor was the connection with food obvious at first. Indeed, the chimpanzees showed little interest in the apparatus and did not perform the desired behavior throughout baseline sessions conducted before training of a model. Only after they had observed another chimpanzee complete the series of actions did many individuals adopt unambiguously the method specific to the group in which they lived.

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THE SOCIAL SIDE OF PRIMATE CULTURE

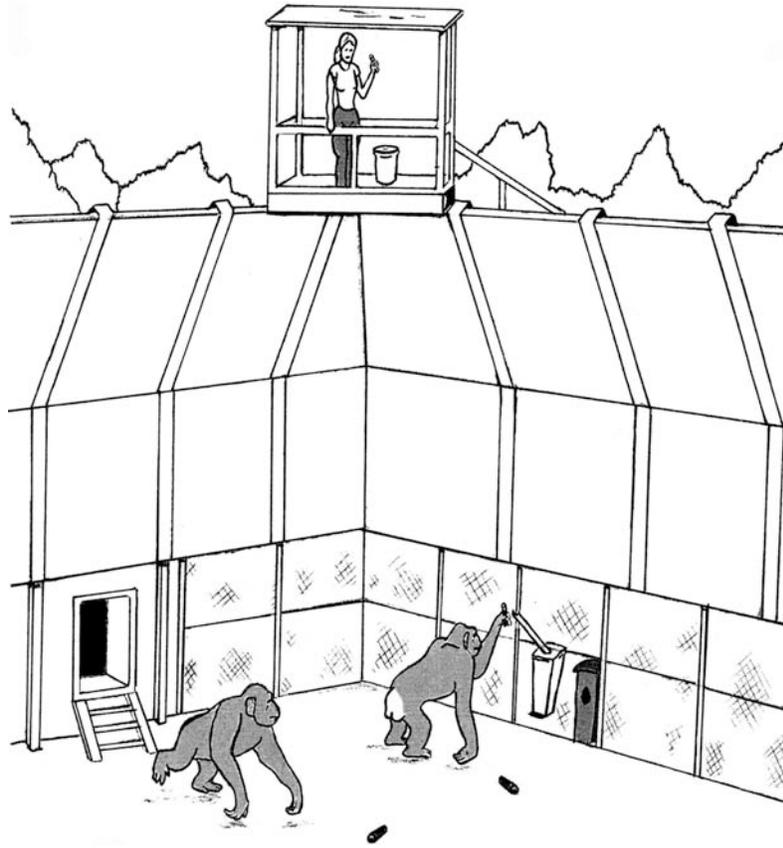


Figure 2.6 Chimpanzees in a large outdoor compound are rewarded by an experimenter positioned on an observation tower for depositing tokens into either of two receptacles on the right. From Bonnie et al. (2007). Drawing by Devyn Carter.

We provided chimpanzees with two dozen tokens constructed from PVC pipe—objects that are familiar enrichment items for our chimpanzees and have been used in previous experiments (Brosnan and de Waal 2005). Tokens were scattered throughout the compound, a large outdoor area to which the chimpanzees have free access. In addition, two unique “receptacles,” a bucket and a chute, in which tokens could be placed were available. The experimenter stood on a platform 6 meters above the scene so as not to bias the chimpanzees toward the location of either receptacle (Figure 2.6).

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To obtain a reward, chimpanzees needed to complete a five-step behavioral sequence that included searching for a token in the compound, picking it up and transporting it to the receptacles, inserting (and letting go of) the token into either the bucket or chute, and finally looking up toward the experimenter for a reward. A high-ranking adult female from each group was trained to deposit tokens in one of the two receptacles, although both receptacles were always available and both yielded equal rewards to all.

As a result of observing a conspecific model interact with the tokens and receptacles in a meaningful way, two different but equally rewarding conventions spread to become traditions in both groups. Because both receptacles were available and yielded equal rewards, it is unlikely that all individuals in a single group would have discovered just one of the receptacles on their own. Thus we have demonstrated that chimpanzees are capable of perceiving the benefits associated with an initially meaningless action chain performed by a conspecific model, and of duplicating the entire chain so as to gain the same reward (Bonnie et al. 2007).

Conclusion

To understand the mechanisms of social transmission that underlie animal (and human) culture, we need to move beyond the learning paradigms developed on individually tested laboratory animals. Not that individual experience plays no role. Rewards for individual performance definitely exert a major influence on the speed of behavioral acquisition and the maintenance of behavior. But this is usually not how social learning starts. It starts with paying attention to others, often literally being “in their face” (Figure 2.7), watching every move they make. It is here that identification with the other and being socially close matter. One might downplay this as merely the attentional level, but there is more to it. There are many examples of unrewarded behavior that is nevertheless copied from others (e.g., handclasp grooming, the opening of boxes in our monkey experiment). This means that acting like others has its own intrinsic motivation, regardless of external reinforcement. Social learning is more, therefore, than individual learning in a social context: it is subject to powerful social modifiers and motivators.

A good example, apart from the multitude of examples provided in this chapter, is the “conformism” suggested by Whiten et al. (2005), who

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Figure 2.7 Watching adults is a favorite activity of young chimpanzees and is thought to be the way they gain knowledge about sources of food and feeding techniques, such as this female's way of picking grubs out of rotten wood. Photograph by Frans de Waal.

found indications that even if chimpanzees discover an alternative solution to a problem, they nevertheless converge on the “culturally” prevailing solution. We have found additional suggestions for this effect, which, if confirmed, would nicely fit the BIOL model but not the other models of social learning.

This has implications for how cultural learning research on primates is being conducted. Instead of using human models, for example, we conduct all of our experiments with conspecific models. And instead of looking at social learning as mainly a cognitive issue, we have ample evidence that it is very much part of social relationships, requiring bonding, identification, and tolerance. Even though traditional learning paradigms undoubtedly need to be part of any cultural learning framework, we suggest that social relationships and close observation of certain “role models” will need to be part of it as well, at least for the many social mammals that live in highly individualized societies.

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