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During the past decade, researchers working in a variety of subdisciplines within anthropology, psychology, and biology have made substantial progress in their study of imitative and nonimitative forms of social learning in animals. Nonimitative social learning is now known to play an important role in reproduction, food acquisition, and predator avoidance in a range of vertebrate species. Evidence is also available that not only great apes but also some birds and nonprimate mammals can learn by imitation.

Social Learning and Imitation

Why Study Social Learning?

Most scientists who study animal social learning are interested in one of two quite different issues. Primatologists and psychologists frequently want to know whether nonhuman animals are able to imitate behaviors that they have seen others perform. For these researchers, situations in which one animal can learn to do an act simply by watching another animal perform that act provide exciting opportunities to explore the cognitive abilities of species other than our own. Other researchers, those whose work on social learning in animals reflects a general interest in behavioral ecology, usually study social learning to understand how information acquired from others contributes to the development of adaptive patterns of behavior in free-living animals. These researchers are interested in social interactions that direct behavior in profitable directions regardless of whether imitation or some nonimitative social learning process that is less cognitively demanding than imitation is believed to support transmission of behavior from one animal to another. Both approaches to the study of social learning are useful, and both have venerable histories in the life sciences.

Since the end of the nineteenth century, there have been many attempts to define different types of social learning and to categorize instances of social learning in terms of the learning process on which each depends. Sometimes social learning seems to involve true imitation (learning to do a particular motor act from seeing it done), whereas other times it appears to rest on emulation (learning what is required for success in a task by watching a model perform, but not learning about the model's behavior per se; Tomasello, 1996), local enhancement ("apparent imitation resulting from directing the animal's attention to a particular object or part of the environment"; Thorpe, 1963, p. 134), or some other carefully defined behavioral process (Galef, 1988b; Whiten and Ham, 1992). Different types of social learning are believed to require different degrees of cognitive sophistication, so the question of what type of social learning is involved in the transmission of behavior from one individual to another has potentially important implications for our understanding of the cognitive abilities of animals.

Historically, the most important distinction, and the only one I make in this article, involves determining whether, in any particular case, an observer learns directly about the behavior of its model. In the various kinds of nonimitative social learning, an animal that watches another animal behave and sees the outcome of the behavior in which the actor engages learns something useful about either which parts of the environment are potentially important or what changes in the environment are caused by the actor's behavior (Heyes, 1996; Tomasello, 1996). Therefore, for example, if one chimpanzee were to watch another hunting grubs by turning over logs using its left hand to flip the logs end over end, the observing chimp might learn (i) that logs are interesting objects (learning about the environment), (ii) that food is revealed when the undersides of logs are exposed (learning about changes in the environment that the behavior causes), or (iii) that putting one's left hand under the end of a log and moving that hand rapidly upward is rewarded with food (learning about the actor's behavior). Only the last kind of learning, in which the observing chimpanzee learns directly about the behavior of the acting chimpanzee, would involve true imitation as imitation is currently defined (Heyes, 1996; Tomasello, 1996). Such "true" imitative learning seems to require that an animal or human first store a visual representation of the pattern of movement exhibited by another. Then, because the imitator rarely sees its own movements in a way that would allow it to match the sight of its limbs moving to the stored visual representation of the act to be imitated, the imitator must use its proprioceptive or kinesthetic senses to match its own movements to the stored visual representation. Such cross-modality matching is believed to be a cognitively demanding task that distinguishes true imitative learning from other possibly less complex, nonimitative forms of social learning.

Nonimitative Social Learning

Perhaps the simplest way to introduce outsiders to recent advances in the study of nonimitative social learning is to briefly describe a selection of recent analyses of socially learned behaviors with potential to contribute to survival or reproductive success. I chose the examples discussed here to indicate both the range of behaviors affected by nonimitative forms of social learning and the very different ways in which information acquired from others can facilitate acquisition of adaptive patterns of behavior.

Learning What to Eat: Food Selection and Poison Avoidance by Norway Rats

Decades ago, an applied ecologist trying to increase the efficiency with which rodent pests could be controlled discovered that when he repeatedly offered a single poison bait to any population of rats (*Rattus norvegicus*), his efforts at control failed dismally. Although there was a decline in rat numbers immediately after he introduced a poison bait into an area, target populations repeatedly exposed to the same bait soon recovered their original size. The reasons for failure when using a single bait repeatedly in the same area were fairly straightforward.

First, although most rats ate a lethal dose of a toxic bait shortly after it was first introduced into their colony's territory, a few members of most colonies ate only a small amount of bait the first time they tasted it, became ill, but did not perish. These surviving rats learned in a single trial to associate the taste of the bait with its ill effects, and they would eat no more of it.

Second, and even more discouraging for efforts to improve the economics of pest control, young rats that came of age in colonies whose members were survivors of a first encounter with a poison bait also totally rejected the bait that the members of their colony had learned to avoid. They would eat only foods that survivors were eating. Somehow, the poison avoidance learned by survivors was being transmitted to the young of their colony.

Such socially learned avoidance of poison bait by weaning rats is a robust phenomenon and is easy to capture in the laboratory (Galef, 1988a). Consequently, it has proven possible to explore in-depth the social learning processes that result in transmission of food choices from adult rats to juveniles of their species.

Potential Prenatal Influences on Flavor Preference Even before birth, a young rat can acquire information from its female parent about at least some of the foods that she is eating. Hepper (1988) fed garlic to pregnant rats late in gestation. An hour or less after litters were delivered by these garlic-fed mothers, Hepper gave the young to foster mothers that had never eaten garlic to rear. When the foster-reared pups were 12 days old and still ingesting only mother's milk, Hepper offered them a choice between two dishes, one containing garlic and the other onion. He found that pups that had been gestated by mothers that ate garlic while pregnant stayed near the dish containing garlic, whereas pups gestated by mothers that had not eaten any garlic during pregnancy did not prefer garlic to onion.

Flavor Cues in Mothers' Milk Flavors of foods that a rat eats while lactating can affect the flavor of her milk, and exposure to flavored milk affects the food preferences of rat pups as they wean. For example, weaning rat pups preferred the food eaten by a lactating female from whom they had suckled for several hours but did not prefer the same food after they interacted\ for the same length of time with a female that ate the same food and acted maternally toward the pups but did not give milk (Galef, 1977).

Effects during Weaning Galef and Clark used closed-circuit television and time-lapse video recordings to observe nine wild rat pups from three litters take their very first meals of solid food. All nine pups were observed to eat for the first time in exactly the same circumstances: Each ate at a site at which an adult was eating, and none ate at a nearby site at which no adult was present. Apparently, the physical presence of an adult rat at a feeding site made that site attractive to young rats and markedly increased the probability that they would wean to whatever food was to be found there (Galef, 1977). Indeed, simply anesthetizing an adult rat and placing it, while unconscious, near a feeding site made that site significantly more attractive to weaning rats than alternative locations that had no rat near them.

However, adult rats need not be physically present at a feeding site to guide their young to it. While eating, adult rats deposit residual olfactory cues in the vicinity of a food source, on any food they eat, and on the path they take when leaving a feeding site and returning home. All these odorants are attractive to young rats and cause them to approach and prefer feeding sites that adults have been using (Galef, 1977).

Effects after Weaning Galef and his students also found that after a young rat (an observer rat) interacts for a few minutes with a recently fed conspecific (a demonstrator rat), the observer exhibits a substantial increase in its preference for whatever food its demonstrator ate (Galef, 1988a, 1996). Exploration of the processes responsible for development of this socially induced preference in observer rats began with the finding that when observer rats were exposed to anesthetized demonstrator rats whose heads had been lightly dusted with particles of food (Fig. 1), the observer rats increased their preference for the food that they found on their respective demonstrators' heads. On the other hand, observer rats identically exposed to pieces of cotton wool dusted with food failed to develop a preference for that food (Galef, 1988a). Clearly, something about the presence of a demonstrator rat together with a food causes observer rats to alter their food preferences.

Experiments to discover the stimuli emitted by demonstrator rats that cause observer rats to increase their preference for foods associated with a demonstrator have shown that exposure to a constituent of rats' breath, carbon disulfide, and a food causes rats to increase their preference for the food, just as experience of a food together with a breathing rat increases preference for it (Galef, 1996).

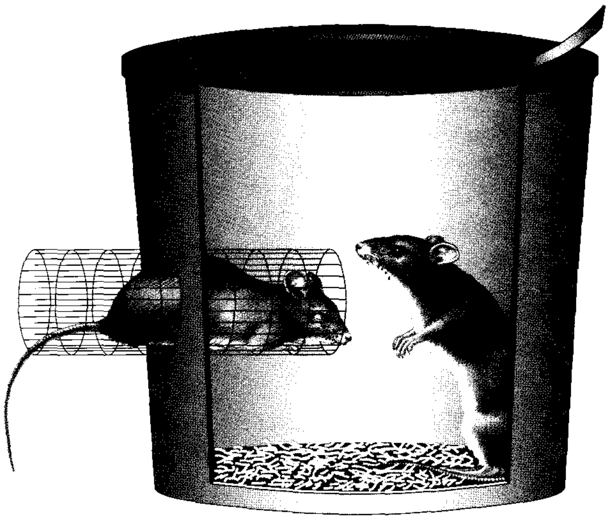

FIGURE 1 An observer rat interacts with an anesthetized demonstrator rat whose head has been dusted with food (adapted from Galef and Stein, 1985).

Learning How to Eat: Exploitation of Pinecones by Roof Rats

The pine forests of Israel are inhabited by colonies of roof rats (*Rattus rattus*) that live on a diet consisting almost entirely of pine seeds and water (Terkel, 1995). Extraction of seeds from pinecones is a stable tradition in these rat colonies, permitting them to survive in areas in which pine seeds are the only food present in sufficient quantity to support a population of mammals.

Laboratory observations of the feeding behavior of rats taken from colonies living in pine forests have shown that the feeding method that allows rats to recover more energy from pine seeds than they spend in removing the tough, nonnutritious scales from pinecones requires that the rats take advantage of the structure of pinecones. The scales at the base of a cone must be removed first. Then the spiral of scales circling the cone's shaft to its apex must be removed in succession (Fig. 2).

Observation in captivity of rats taken from areas other than pine forests and offered pinecones to eat revealed that only 6 of 222 hungry, adult rats learned to use the spiral pattern of scale removal that permits a net energy gain from eating pine seeds. On the other hand, essentially all young rats reared by dams that efficiently stripped seeds from cones acquired the profitable technique. Apparently, some aspect of the interaction between mothers that strip seeds from pinecones and the young they rear is important in transmission of the efficient technique from one generation of rats to the next.

Further experiments demonstrated that experience of young rats in completing the stripping of scales from cones that had been started in the proper fashion by an adult rat (Fig. 3) allowed more than 70% of young rats to learn the efficient method of attacking cones (Terkel, 1995).

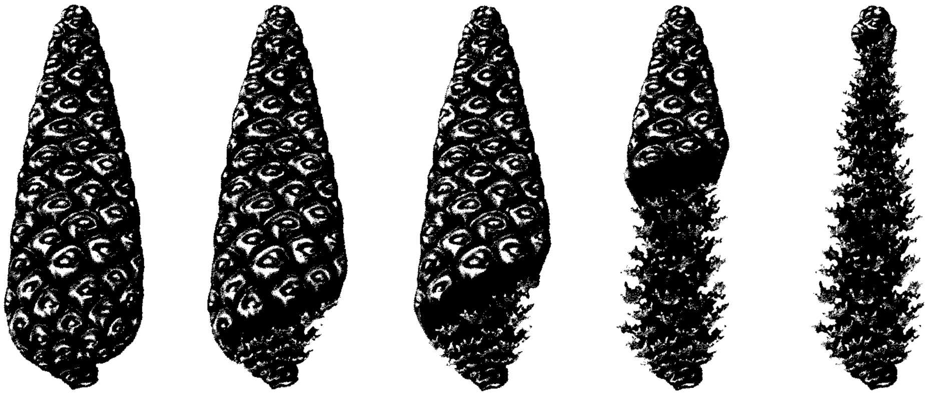

FIGURE 2 Sequence of the stripping of scales from a pinecone by a rat: from left to right, the scales are removed from the base to the top following their distribution on the cone (adapted from Heyes and Galef, 1996).

The tradition of pinecone exploitation seen in these forest-dwelling roof rats is of particular interest because it allows rats to thrive in a relatively sterile environment that would otherwise be closed to them. In this case, and perhaps in others as well, social learning has opened a new ecological niche to some members of a free-living species.

Learning What to Fear: Snake Avoidance by Rhesus Monkeys

How animals learn to avoid predators is difficult to understand because building an innate system to distinguish all harmless animals from all potentially dangerous animals seems almost impossible, given the wide range of predators to which many animals are vulnerable, and because learning to avoid predators by individual experience would not work very well either. Predators must be avoided the first time they are encountered. There is no time for trial-and-error learning.

It has been known for more than 40 years that although monkeys and apes that have been captured in the wild and brought into the laboratory will vigorously avoid contact with snakes or snake-like objects, monkeys born and reared in captivity are relatively indifferent to the same objects that elicit strong fear responses in their wild-born brethren.

Mineka and Cook (1988) studied effects on the responses of laboratory-reared monkeys to snakes after these monkeys watching wild-born monkeys exhibit their fear of snakes. They found that laboratory-reared monkeys, which initially showed little or no response to snakes, responded vigorously to the sight of a snake after seeing a wild-reared monkey respond to a snake. This effect on the responses of laboratory-reared monkeys to snakes did not diminish over 3 months.

It is interesting to note that monkeys would not learn to respond emotionally to any object to which they watched a conspecific react. When Mineka and Cook (1988) showed laboratory-reared monkeys videotapes of wild-reared monkeys exhibiting fear responses elicited by snakes but edited the videotapes so that the monkeys appeared sometimes to be exhibiting fear of snakes and other times to be exhibiting fear of flowers, the laboratory-reared monkeys learned to fear the snakes but not the flowers. Apparently, the mon-

FIGURE 3 A rat pup feeding near its mother on a pinecone she has started to strip.

keys learned selectively to associate snake-like objects with the fear responses of others of their species.

Learning with Whom to Mate: Choice of a Partner by Guppies

Although evidence of a role for social learning in the development of adaptive patterns of response to potential foods and potential predators is more than 20 years old, direct evidence of a role for social learning in selection of a sex partner was only recently obtained. Dugatkin and coworkers (Dugatkin, 1996) examined the role of social learning in mate choice by the wild relatives of the aquarium guppy (*Poecilia reticulata*). Guppies were selected as subjects for two reasons. First, the conditions under which guppies mate in the streams of Trinidad (where the guppies used in these experiments were captured) were such as to allow social influences on mate selection to occur. Second, guppies are relatively easy animals to breed, maintain, and observe in the laboratory.

In Dugatkin's experiments, an aquarium was placed between two water-tight end chambers, and at each end chamber was placed one of a pair of male guppies matched for size and overall brightness (qualities that are attractive to females of their species). A "subject" female was then placed in a clear container in the center of the aquarium and a second female, a "model" female, was confined by a glass barrier at one end of the aquarium near one of the two males.

Once the experimental situation had been set up, the subject female could watch as the male closer to the model female was allowed to court the model female for 10 min. At the end of the 10-min period of courtship, the model female and the barrier that had kept her at one end of the aquarium were both removed from the aquarium, and the subject female was released from confinement and was then allowed to choose between the two males in their end chambers. Of the 20 subject females that Dugatkin observed choose a male in this situation, 17 chose to stay near the male they had watched courting the model female.

Although the results of this first experiment were consistent with the hypothesis that female guppies copy one another's mate choices, there are several alternative explanations of the model females' preference that need to be examined before that hypothesis is accepted. For example, it is possible that female guppies, members of a species that in the wild tends to form shoals, might simply prefer an area in which they had previously seen two fish to an area in which they had previously seen only one fish. However, in an experiment identical to that described previously except that females rather than males were placed in the two end chambers of the apparatus, subject females chose the female in the end compartment near which the model female had been confined only 10 times out of 20, as would be expected by chance (Dugatkin, 1996).

Dugatkin's data demonstrate a strong social influence on mate choice by female guppies. His findings are also consistent with explanations that have been proposed for some intriguing behavioral phenomena observed in natural circumstances. For example, in species such as sage grouse, in which males compete directly for females on communal breeding grounds (leks), each day a few males enjoy access to almost all females. Details of the circumstances in which sage grouse mate in natural circumstances are consistent with the hypothesis that female grouse observe and copy the mate choices of others, leading to near unanimity in mate selection by hens on any day (Gibson *et al.*, 1991).

Even more puzzling is the observation that males of some fish species court and readily mate with females of other species, even though males mating with these females do not contribute any genetic material to the females' young. Schlupp *et al.* (1994) followed up on Dugatkin's observations of social influence on mate choice by female guppies and found that male sail-fin mollies, which frequently mate with females of another species (the Amazon molly), actually increase their access to females of their own species by such cross-species matings. Female sail-fin mollies tend to prefer males they have seen mate, even when the males mated with female Amazon mollies.

Learning How to Court: Song Learning in Brown-Headed Cowbirds

Brown-headed cowbirds (*Molothrus ater*) are particularly interesting to students of social influences on behavioral development because females of this species lay their eggs in nests constructed by members of other species (the brown-headed cowbird is "brood parasitic"). Consequently, young brown-headed cowbirds are always reared by foster parents that are members of some other species. A young cowbird has no contact with adults of its own species while growing up. Because of the isolation of juvenile from adult cowbirds, it was long thought that song learning by male cowbirds was not affected by social interaction. However, as a result of the insight and hard work of Meredith West and Andrew King, it is now clear that young male cowbirds, like the young of many other species of songbird, learn the fine details of their songs as a result of social interaction.

Male cowbirds from different geographical areas sing different variants of cowbird song, and these "song dialects" are maintained by differences in the responses of females from different areas to the songs that males produce. The same songs that, during the breeding season, are most likely to cause females to assume the "copulatory posture" that allows males to mate (Fig. 4b) are responded to by females at other times of the year with a "wing-stroke" display (Fig. 4a). After a female gives a wing stroke in response to a song, the male singing that song repeats it three or four times in succession, violating a basic rule of song produc-

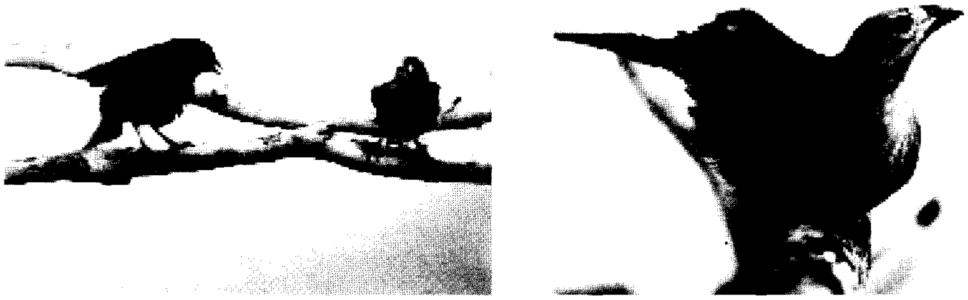

FIGURE 4 A female brown-headed cowbird giving the wing-stroke display (a) and exhibiting the species-typical copulatory posture (b) in response to a singing male.

tion by male cowbirds; normally, a male cowbird sings the various songs in his repertoire one after another without repetition. Seeing a female give wing strokes increases not only the frequency with which a male sings a song outside the breeding season but also the frequency with which he sings that song within the breeding season, thus increasing his potential breeding success (West and King, 1996).

More surprising, the songs that male cowbirds sing are also influenced by interactions with male cowbirds. Song variants most effective in eliciting copulatory postures in female cowbirds are also most effective in eliciting attacks by male cowbirds. Consequently, only the dominant males in a group can continue singing the song variants most effective in eliciting copulation postures from females without suffering severe injury from males.

Summary

There are two basic lessons to be drawn from the preceding descriptions of instances of nonimitative social learning in animals: First, such social learning can play a role in the development or maintenance of many patterns of behavior that contribute to fitness. Second, there are many fundamentally different behavioral processes that support social learning. Food preferences of Norway rats are affected by exposure of rats to the odor of foods in combination with chemicals carried on rats' breath. Complex feeding techniques are learned by young roof rats as a result of exposure to food items partially opened by knowledgeable adults. Female guppies mate with males that have recently courted other females, and male cowbirds learn the most effective songs to sing as the result of receiving enticements from females and punishments from males.

Although the behavioral processes that support the various instances of social learning discussed previously differ considerably, none is the result of learning to do an act by seeing it done. None is an instance of learning by imitation, the subject of the second part of this article.

Imitation

The descriptive literature is rich in informal observations suggesting that animals from chimpanzees (reported to learn to open paint cans, sharpen pencils, and use sandpaper) to dolphins (reported to have copied a diver cleaning the windows of their aquarium) can learn complex motor patterns by imitation (Moore, 1992). Although the descriptions of such human-like behaviors in animals are very likely accurate, there are two basic problems with accepting them as basic data for understanding the abilities of animals. First, without formal observation it is very difficult to determine how frequently animals engage in such apparently imitative behaviors. Consequently, it cannot be determined if they are just chance correspondences between the behaviors of a caretaker and an animal seen when millions of people watch millions of animals behave every day. Tens of millions of people own pets and see them behave for hours each day, but it is only on those rare instances when an animal appears to have spontaneously copied a behavior demonstrated by its caretaker that a report of the behavior is made to others. No one reports the countless millions of times when pets see their caretakers engaging in a useful behavior but fail to copy it (Visalberghi and Fragaszy, 1990).

Second, it is difficult to determine from observations made in uncontrolled environments how human-like behaviors developed in those animals that exhibit them. Did the presumed imitator actually observe a behavior and then produce it, or did it have its attention focused on some object, for example, a door, by the behavior of a caretaker and then try tens or hundreds of times to open the door before succeeding?

To avoid problems inherent in using chance observation of potentially interesting behavior to study imitation, scientists tried to find situations in which animals living in the behavioral laboratory under controlled circumstances would imitate. For the first 90 of the 100 years that such efforts were under way, behavioral scientists were almost entirely unsuccessful in getting animals to learn by imitation when nonimitative types of social learning were prevented. Not surprisingly, given such prolonged failure, many researchers concluded that, regardless of informal reports to the contrary, nonhuman animals were probably not able to learn by imitation. However, a few scientists remained concerned by the lack of agreement between the formal and informal evidence of imitation learning in animals. It is this group that is ascendent today because the past decade has seen an accumulation of experimental evidence that, taken together, offers considerable support for the view that a wide variety of animals may be able to learn by imitation.

Making Observation out of Anecdote: Field Studies of Orangutan

Russon and Galdikas (1993) worked in a camp in Borneo in which orangutans that had been captured by poachers and reared in captivity were prepared by conservationists for return to life in the wild. Russon and collaborators systematically observed, and sometimes were able to videotape, any apparently imitative behaviors exhibited by the apes as they moved in and out of camp and interacted with its human inhabitants. Russon and Galdikas described dozens of complex human behaviors that the apes appeared to copy. For example, an adult female orangutan was seen in a lean-to in which fuel drums were kept. Camp staff regularly siphoned fuel from drums into cans by first opening the lids of both a fuel drum and can, then inserting one end of a hose into the fuel drum, getting the fuel to flow by sucking on the other end of the hose, and rapidly inserting the end of the hose that had been sucked on into the can. The ape was observed while she unscrewed the caps from both a fuel drum and can, inserted one end of a hose into the fuel drum, placed the other end of the hose in her mouth, and bellowed her cheeks. After much manipulation of the hose and fuel drum, she inserted the hose end that had been in her mouth into the open can. Although the fuel drum the orangutan had selected was empty, and the timing between sucking on the hose end and inserting it into a can was inappropriate, the sequence of acts was similar to that of a human siphoning fuel.

Although it is not possible to know, in uncontrolled circumstances, just how the ape came to exhibit such behavior, the many instances of apparent imitation that Russon and Galdikas describe suggest that orangutans can imitate in appropriate circumstances. Indeed, Russon and Galdikas's observations even provided a clue regarding circumstances that increase the likelihood that orangutans will spontaneously imitate humans. Analyses of observations made in the jungles of Borneo showed that a close social relationship between human model and ape mimic increased the probability of spontaneous imitation by apes. Given this result, it is not surprising that some of the most promising recent laboratory studies of imitation of humans by apes have used as subjects apes reared in intimate contact with humans.

Imitation by "Enculturated" Chimpanzees

Tomasello and colleagues studied imitation learning by enculturated chimpanzees that had been raised by humans and given instruction in human-like languages, by 2-year-old human infants, and by chimpanzees reared by their own mothers. All subjects watched while a human model demonstrated a series of novel actions directed toward objects. For example, subjects saw a human model place a ball on his head and use a lever to pry open the lid of a paint can. The children were told "Do this" and the apes had been pretrained to reproduce familiar actions modeled by a human demonstrator (Tomasello, 1996). The results of Tomasello's experiment were clear: Apes reared by their natural mothers failed almost totally to imitate the novel actions the experimenter demonstrated. Two-year-old children and enculturated apes imitated the experimenter's actions equally often and with considerable frequency. Tomasello's experiment is but one of several pointing to the same conclusion. Recently, evidence consistent with the view that chimpanzees raised by humans are able to imitate novel actions demonstrated by a human model has been found in many laboratory situations (Whiten and Custance, 1996).

Imitation by Animals Other Than Apes: Norway Rats, Pigeons, Quail, and an African Gray Parrot

The results of other recent experiments indicate that not only great apes but also a variety of less likely animals seem able to reproduce simple motor acts after observing others engage in them. In a series of studies, Heyes and coworkers let observer rats watch through a screen partition while a rat trained to push a joystick suspended from the cage ceiling either to the left or to the right pushed the joystick 50 times in succession in the appropriate direction and received a food reward for each displacement. Then, the demonstrator rat was removed from the apparatus, and an observer rat was placed in the compartment containing the joystick and was allowed to push it 50 times, receiving a food reward following each displacement of the joystick in either direction. For some observers, the joystick remained in the same position during both training and testing; for others, the joystick was moved before each observer was tested from near the screen partition to the front wall of the chamber (Fig. 5). Under both conditions, each observer rat tended to push the joystick in the same direction relative to its own body axis, as had its demonstrator (Heyes, 1996). Zentall and students reported similar imitation by pigeons and quail.

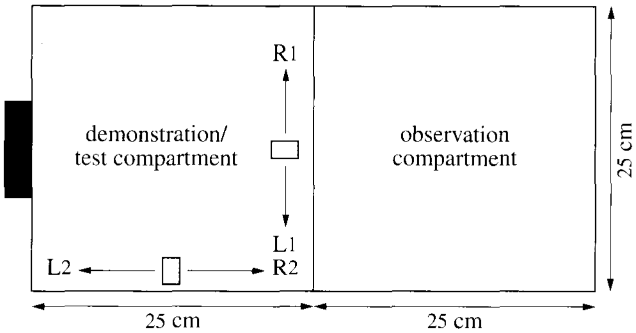

FIGURE 5 Schematic of the apparatus used by Heyes in the search for imitation learning in rats. The diagram shows the joystick in its starting position (between R1 and L1) and in the position to which it is moved for some observers during the test (at the front of the cage, between R2 and L2). An observer rat that saw a demonstrator move the joystick to R1 moved it toward R1 or R2 during testing — that is, in the direction used by the demonstrator. (adapted from Heyes *et al.*, 1992).

Moore (1992) provided startling evidence of spontaneous imitation of a human by an African gray parrot (*Psittacus erithacus*) that he named Okichoro. Moore housed Okichoro alone in a room that contained, along with the usual perches and toys, a microphone and video camera that allowed observation of Okichoro's behavior when alone and undisturbed.

Moore visited the aviary several times a day during a period of 5 years. During each visit, he repeatedly performed many distinct movements, each accompanied by a different spoken word or phrase. For example, as Moore left Okichoro's aviary each day he waved good-bye and said "ciao." Okichoro soon learned to say "ciao" and, by the end of the first year, was observed alone in his room saying "ciao" and at the same time waving his foot.

When in Okichoro's aviary, Moore also said "Look at my tongue," opened his mouth, and stuck out his tongue. Some time after Okichoro started to say "ciao" and wave, he was observed on the television monitor saying "Look at my tongue" and then opening his mouth and raising his tongue. Okichoro rarely opened his mouth and raised his tongue after saying "ciao" or waved his foot after saying "look at my tongue." In all, Okichoro was observed to copy many different actions involving six different body parts and to associate each action with its appropriate label (Fig. 6).

Some scientists accept such studies of social learning in nonprimates as providing examples of true imitation. Others reject them as examples of true imitation because it is difficult to know whether the motor patterns that the subjects used to produce a model's behavior were novel. It is possible that the acts that the animals copied were already in their behavioral repertoires and that they learned by observation only when to engage in acts they already knew how to perform. Whether production by an animal of an act already in its repertoire when it sees another animal perform that act should be considered true imitation is not clear. Difficult theoretical work remains to be done to reach consensus about exactly how imitation should be defined

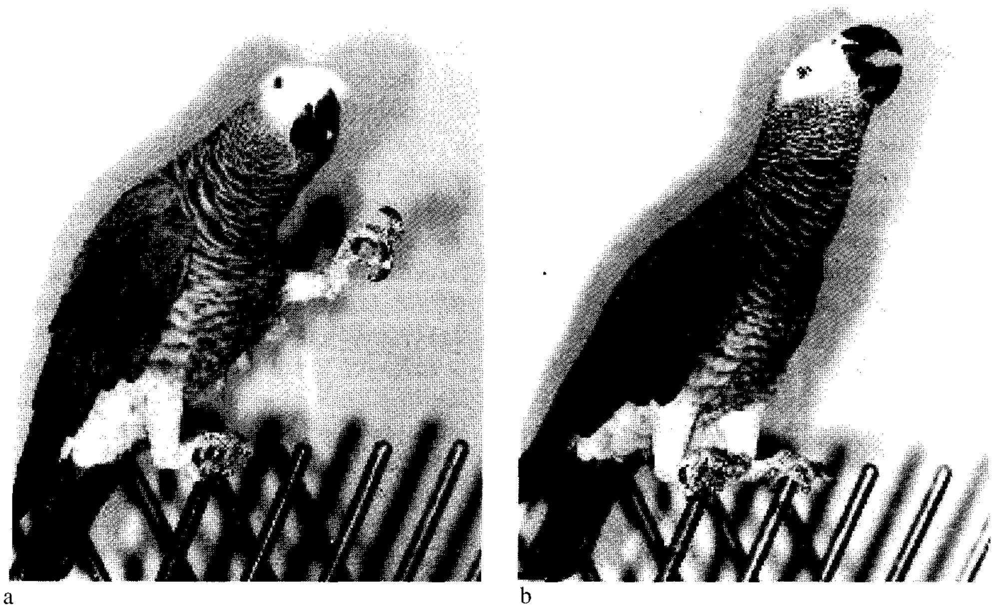

FIGURE 6 Examples of the imitation of human movements by the parrot Okichoro: (a) The parrot said "ciao" and (b) "look at my tongue" (adapted from Moore, 1992).

and what can be inferred regarding the cognitive abilities of animals from demonstrations of imitation of familiar or novel acts.

Conclusion

These are exciting times for students of imitative and non-imitative social learning in animals. After 100 years of effort, we may finally be in a position to start to explore the cognitive processes supporting imitation learning in animals and to compare such processes with those supporting imitation learning in humans. After all, even if both humans and apes imitate, they may not do so in the same way.

There is also strong evidence of an important role for social learning in the development of patterns of behavior that facilitate survival and reproduction by animals living in natural habitat. Such findings make important contributions to our understanding of the sources of information that animals use to respond adaptively to the challenges posed by their environments.

Two decades of hard work by scientists in many disciplines are starting to pay off. The next decade of research in social learning and imitation promises to be at least as productive as the past.

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