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CHAPTER TWELVE

Recent progress in studies of imitation and social learning in animals

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The last two decades have seen remarkable progress in the study of social learning and imitation in animals. Emergence of the field as a dynamic interdisciplinary area of inquiry has been the result of three separate developments: (1) Behavioral ecologists and experimental psychologists have found both in one vertebrate species after another and in one biologically important situation after another that information acquired from conspecifics facilitates development of adaptive patterns of behavior. (2) After nearly a century of effort, primatologist and comparative psychologists have finally succeeded in providing compelling evidence that nonhuman animals can learn by imitation, and (3) population biologists and behavioral ecologists have developed quantitative models that permit exploration of the selective pressures that result in animals depending on social learning in developing responses to environmental demands. Here I review, albeit briefly, the three research streams that have contributed to the recent metamorphosis of the field.

L'étude de l'apprentissage social et de l'imitation chez l'animal a connu un essor remarquable au cours des deux dernières décennies. L'émergence du domaine en tant que champ de recherche interdisciplinaire repose sur trois axes d'évolution. (1) Chez plusieurs espèces de vertébrés et dans plusieurs situations importantes sur le plan biologique, les écologistes comportementaux et les psychologues expérimentalistes ont constaté à répétition que l'information obtenue à partir des congénères facilite l'apparition de patrons comportementaux adaptatifs. (2) Après près d'un siècle d'effort, les primatologues et les chercheurs en psychologie comparée ont finalement réussi à dégager des indices convaincants de la capacité qu'ont les animaux non humains d'apprendre par imitation. (3) Les biologistes spécialistes des populations et les écologistes comportementaux ont élaboré des modèles quantitatifs permettant d'examiner les pressions sélectives qui font que les animaux dépendent de l'apprentissage social dans la production de réponses aux exigences de l'environnement. Bien que ce soit de manière brève, les trois courants de recherche ayant participé à la récente métamorphose du domaine sont ici analysés.

These are exciting times for those of us interested in the study of animal social learning. During the past 20 years, the field has changed remarkably. It has metamorphosed from a rather sluggish subarea of animal learning into a fast-moving, independent, often disputatious area of inquiry that has captured the attention of empiricists and theoreticians working in a range of disciplines from anthropology, through experimental psychology and behavioral ecology to theoretical biology.

Formal evidence of the current high level of activity in the study of social learning in animals is plentiful: Review chapters (Galef, 1988, 1996b; Fragaszy &. Visalberghi, 1996; Heyes, 1994; Mitchell, 1989; Whiten & Ham, 1992), edited volumes (Heyes & Galef, 1996; Wrangham, McGrew, de Waal, & Heltne, 1994; Zentall & Galef, 1988), theoretical articles (Coussi-Korbel & Fragaszy, 1995; Galef, 1995; Heyes, 1994), and even book-length monographs (Bonner, 1980; King, 1994; McGrew, 1992; Wyrwicka, 1996) are now appearing at a steady clip; symposia and conferences on the topic are convened almost annually on both sides of the Atlantic.

Informal indications of a marked increase in activity in the field are, perhaps, even more convincing than is the formal evidence; my stack of reprints published during the 1970s and concerned with social learning in animals measures but 5.2cm in height, comparable materials from the 1990s (with four years still remaining in the decade) already stands 27.6cm tall!

The dramatic change in activity in the field is the result of three distinct developments: First, behavioral ecologists and experimental animal psychologists have been able to show, in one vertebrate species after another, that social interactions can facilitate the development of adaptive patterns of behavior. Second, after nearly a century of effort, primatologists and comparative psychologists have finally provided compelling laboratory evidence consistent with the view that nonhuman animals can learn by imitation. Third, and finally, population biologists and behavioral ecologists have developed quantitative models that permit exploration of the selective forces driving the evolution of social learning.

In sum, in the last two decades, the field of animal social learning has gained a momentum, excitement and energy that were not always characteristic of the area.

A LITTLE HISTORY

During the late 1960s, when I first became interested in problems in social learning and imitation, the area was very much a part of experimental psychology. Almost all experimental work in the area was concerned with demonstrating, in standard laboratory apparatus (Skinner box, T maze, etc.), the existence of general learning processes in animals (e.g. social facilitation, local enhancement, contagious behavior, imitation, etc.) that allowed social interactions to influence the course of individual learning. For example, in a well-known study representative of some of the better psychological research on social learning carried out during the 1960s, Chesler (1969) demonstrated that kittens that had observed their respective mothers press a lever to obtain food subsequently learned to press the lever for food more rapidly than did either kittens that had observed a strange female cat press the same lever for food or kittens that learned to press the lever without the opportunity to watch others do so. In Chesler's view (and apparently that of the editors of *Science* as well) this finding demonstrated that kittens could learn to press a lever by observation, though it is hard to see why the result was so interpreted.

Zajonc (1965) was making much of observations indicating that (1) when racing, two human cyclists moved faster than did either cyclist when riding alone (Triplett, 1897) and (2) ants dug more vigorously when in pairs than when in isolation (Chen, 1937). Zajonc interpreted such diverse findings as examples of a single underlying process, social facilitation (the energizing of dominant behaviors by the presence of others), though even the most naive social scientist must have realized that the processes responsible for social enhancement of human performance are likely to be rather different from those producing a similar result in ants.

Richard Solomon (Solomon & Coles, 1954), Russell Church (1957a,b) and Vaughn Stimbert (1970a,b) had conducted (or were conducting) studies demonstrating that the activities of one animal could serve as discriminative stimuli for another, indicating to the observing animal those occasions on which a particular behavior would be rewarded.

In brief, interesting work was underway, but clearly social influence on animal learning was a side issue, generating relatively few experiments and relatively little excitement.

The late 1960s were a time of unprecedented change in the study of behavior. Within psychology, the influence of behaviorism was on the wane. Concurrently, various biological approaches to behavior were gaining adherents, first in Europe, then in North America. Even within psychology, evolutionary perspectives on animal plasticity were coming to the fore (Rozin & Kalat, 1971) and investigations of processes supporting the development of behaviors that affected survival and reproduction in natural normal habitat (rather than behaviors unique to the laboratory) were becoming increasingly common (Garcia & Koelling, 1966; Marler & Tamura, 1964). Such changes gave new life to the study of imitation and social learning and produced the acceleration of research in the area that is still underway today.

NON-IMITATIVE SOCIAL LEARNING

Indeed so much work on social learning is underway in the 1990s that the best one can do in a brief review is to provide a sample of research reflecting the current diversity of investigations in the area. I begin with description of portions of an ongoing, but quarter-century-old line of research underway in my own laboratory.

Learning what to eat: Food selection and poison avoidance by Norway rats

Some years ago, Fritz Steiniger, an applied ecologist who worked on problems of rodent control, discovered that if he used the same poison bait repeatedly in an attempt to control a pest population of Norway rats (*Rattus norvegicus*), he failed to produce a lasting reduction in the size of the target population (Steiniger, 1950). Despite an initial die-off when poison was first introduced into a colony's territory, the colony soon regained the size it had before Steiniger started his campaign of extermination.

Steiniger's failure (and the rats' success) had two causes: First, despite Steiniger's best efforts, a few colony members almost always managed to survive their initial intake of the poison bait and would eat no more of it (Garcia & Koelling, 1966). Second, and even more unfortunately for Steiniger's efforts at pest control, young rats raised by these survivors refused to eat the bait that the survivors had learned to avoid and never even sampled it for themselves.

This socially induced avoidance of a poison bait is a robust phenomenon, easily captured in the laboratory (Galef & Clark, 1971a). Consequently, it has proved possible to explore in depth several social learning processes (Galef, 1996c, in press), each of which has the potential to contribute to the social transmission of both food preferences and poison avoidance (Galef, 1985) from adult rats to their young.

Physical presence of adults at a feeding site. Galef and Clark (1971b) used a time-lapse video-tape recorder to watch pups born to wild-caught Norway rats take their very first meals of solid food. Each ate: (1) while an adult rat was eating and (2) at the same site where that adult was eating, not at a nearby site where no rats were present. It appeared that the simple physical presence of an adult rat at a feeding site markedly increased the probability that pups would wean to whatever food was to be found there (Galef & Clark, 1971b). And, in fact, we found that simply anesthetizing an adult rat and placing it near a feeding site made that site far more attractive to weaning rat pups than an alternative feeding site that had no rat near it (Galef, 1981).

Further, because wild Norway rats are exceptionally hesitant to eat any foods that they have not previously eaten (Barnett, 1958; Galef, 1970), once a young wild rat had weaned to one food, it was very reluctant to ingest other potential foods that it encountered. Indeed, a young wild rat might wait as long as 5 days before eating, if it had only unfamiliar foods available (Galef, 1970; Galef & Clark, 1971a). Consequently, anything causing rats to wean to a safe food also caused them to avoid eating any poisonous substances present in their environment (Galef, 1985).

Flavor cues on the breath of rats. Galef and his students have also found that after a naive young rat (an observer rat) interacts with a recently fed conspecific (a demonstrator rat), the observer exhibits considerable enhancement of its preference for whatever food its demonstrator ate (Galef & Wigmore, 1983). Exposing observer rats to either olfactory cues escaping from the digestive tract of demonstrator rats or to the smell of bits of food that cling to their fur and vibrissae causes observers to exhibit a marked enhancement of their preferences for the food that their respective demonstrators ate (Galef, Kennett, & Stein, 1985). On the other hand, exposing observer rats to the smell of a food presented on a piece of cotton wool fails to cause young rats to increase their preference for it (Galef & Stein, 1985). Obviously, there is something about smelling a food odor in the presence of a live, breathing rat that causes an observer rat to change its food preferences (Galef & Stein, 1985).

Mass-spectrographic analysis of rat breath revealed the presence of carbon disulfide in the exhalations of rats (Galef, Mason, Pretti, & Bean, 1988), and exposing rats to pieces of cotton wool both dusted with a food and moistened with a few drops of dilute carbon disulfide solution caused them to exhibit an enhanced preference for the food that they smelled on the cotton wool. On the other hand, exposing rats to pieces of cotton wool dusted with food and moistened with water did not affect their preferences for that food (Galef et al., 1988). Apparently, sulfur compounds carried on rat breath can mediate the social enhancement of food preference that we observed in rats.

Research in laboratories around the world has shown that, like the food choices of Norway rats, food choices of blackbirds (Mason & Reidinger, 1981, 1982), sheep and goats (Provenza, Lynch, & Nolan, 1993), cats (Wyrwicka, 1978, 1981), hyenas (Yoerg, 1991), pigs (Nicol & Pope, 1994), rabbits (Hudson & Altbacker, 1993), gerbils and mice (Valsecchi, Choleris, Moles, Cong, & Mainardi, 1996; Valsecchi & Galef, 1989; Valsecchi, Moles, & Mainardi, 1993) can be influenced by interaction with conspecifics. Such research has also revealed that food selection is not the only aspect of feeding behavior open to influence by social interactions.

Learning how to eat: Roof rats in pine forests

Ron Aisner discovered some years ago that the pine forests of Israel are inhabited by roof rats (*Rattus rattus*) subsisting on a diet of pine seeds and water (Aisner & Terkel, 1992). Extraction of pine seeds has been a stable tradition in these forest-dwelling rodents for many generations, enabling them to survive in evergreen forests where pine seeds are the only food available in sufficient quantity to support a population of mammals.

Laboratory studies have revealed that to gain more energy from eating pine seeds than is expended in securing them, rats must take advantage of the structure of pine cones when removing seeds from beneath the tough scales that conceal and protect them. To show a net energy gain from eating pine seeds, a rat must start by chewing through the scales at the base of a cone and then remove, one after another, the spiral of scales running about a cone's shaft to its apex.

Investigations into the way in which this spiral pattern of scale removal is learned by rats have shown that only 2–3% of adult rats could learn by trial and error to use the spiral pattern of scale removal to gain access seeds. The vast majority of hungry rats either ignored pine cones in their cages or gnawed at them in a way that did not permit extraction of more energy from ingesting pine seeds than was expended in gaining access to them.

On the other hand, essentially all young rats developed the efficient technique if they were reared by an adult rat that stripped scales from pine cones efficiently. Clearly, some aspect of the interaction between adult rats that strip pine cones efficiently and the young they rear is important for transmission of the efficient method of cone stripping from one generation of rats to the next (Aisner & Terkel, 1992; Zohar & Terkel, 1992).

Further experiments by Terkel and his colleagues at the University of Tel Aviv demonstrated that more than 70% of young rats developed the efficient method of attacking cones, if they had opportunity to finish stripping cones started and then abandoned either by efficient adult rats or by an experimenter using a pair of pliers to imitate the pattern of scale removal that is used by efficient rats (Aisner & Terkel, 1992).

Even though the tradition of pine-cone opening is not transmitted by imitation or by any other complex social-learning process, it is particularly interesting, because it demonstrates that social learning can open new ecological niches to social learners thus exposing them to new selective pressures.

Learning what to fear: Predator avoidance in birds and monkeys

The development of predator recognition and patterns of predator avoidance have been of interest to comparative psychologists for many decades. However, attempts to understand the phenomena of predator identification and avoidance on the basis either of individual trial-and-error learning (Hull, 1929) or species-typical defensive reactions to sudden stimuli (Bolles, 1970) have been less than totally successful: Predators do not often provide opportunities for members of prey species to learn from their mistakes, and problems of discriminating harmless from predatory species using unlearned perceptual mechanisms seem insurmountable.

Predator avoidance by blackbirds. The first indication that social learning might play a role in development of responses of prey species to their predators was provided by the elegant experiments of Curio and his colleagues in Bochum, Germany (Curio, 1988; Curio, Ernst, & Vieth, 1978) in studies of the effects on conspecifics of species-typical vocalizations that European blackbirds (*Turdus merula*) make when harassing potential predators (mobbing). Using a simple, but ingenious apparatus (see Fig. 12.1), Curio et al. simultaneously presented an owl (a natural predator of blackbirds) to a knowledgeable, wild-caught European blackbird that mobbed the owl and a harmless object (for example, a stuffed song bird or plastic bottle) to a naive, laboratory-reared blackbird.

In Curio's apparatus, the mobbing blackbird seemed to the naive blackbird to be directing its vocalizations toward the harmless object, and in subsequent tests, the naive blackbird responded to the harmless object as though it were a predator, attacking it while emitting mobbing vocalizations.

Curio went on to analyze this socially transmitted behavior as an instance of Pavlovian conditioning. He found that any novel stimulus, whether a stuffed songbird or stuffed owl, elicited mild, unconditioned avoidance responses in naive blackbirds that increased dramatically in intensity once that novel stimulus was experienced together with tape recordings of mobbing vocalizations (Curio et al., 1978). Thus, social learning directed anti-predator responses of naive blackbirds toward those unfamiliar objects that more experienced individuals treated as potential predators. And, as we shall see later, blackbirds are not the only animals that can learn from others of their species what elements in their environment to treat as potentially dangerous.

Fear of snakes in monkeys. It has been known for more than 40 years that although most wild-caught monkeys and apes vigorously avoid contact with snakes, captive-reared primates are relatively indifferent to snakes and snake-like objects. Possibly conditions of life in captivity are so aberrant that captive-reared individuals fail either to develop or to maintain a species-typical, congenital tendency to avoid snakes. On the other hand, captive monkeys may lack some specific experience that they require to develop snake avoidance.

Sue Mineka and her co-workers at the University of Wisconsin (Cook, Mineka, Wolkenstein, & Laitsch, 1985; Mineka & Cook, 1988) have shown that monkeys reared in captivity and, therefore, without fear of snakes, are terrified of snakes after they see wild-born conspecifics respond to a snake. After laboratory-reared rhesus monkeys (*Macaca mulatta*) watched a wild-reared monkey respond vigorously to the sight of a snake, the laboratory-reared rhesus responded to the appearance of a snake or snake-like object by cowering on the far side of their respective cages and appeared extremely upset, vocalizing and grimacing.

Mineka et al.'s studies contribute substantially to an understanding of how predator recognition and avoidance might develop in free-ranging primates, just as Curio's findings provide a plausible mechanism for understanding the possibly homologous process in birds.

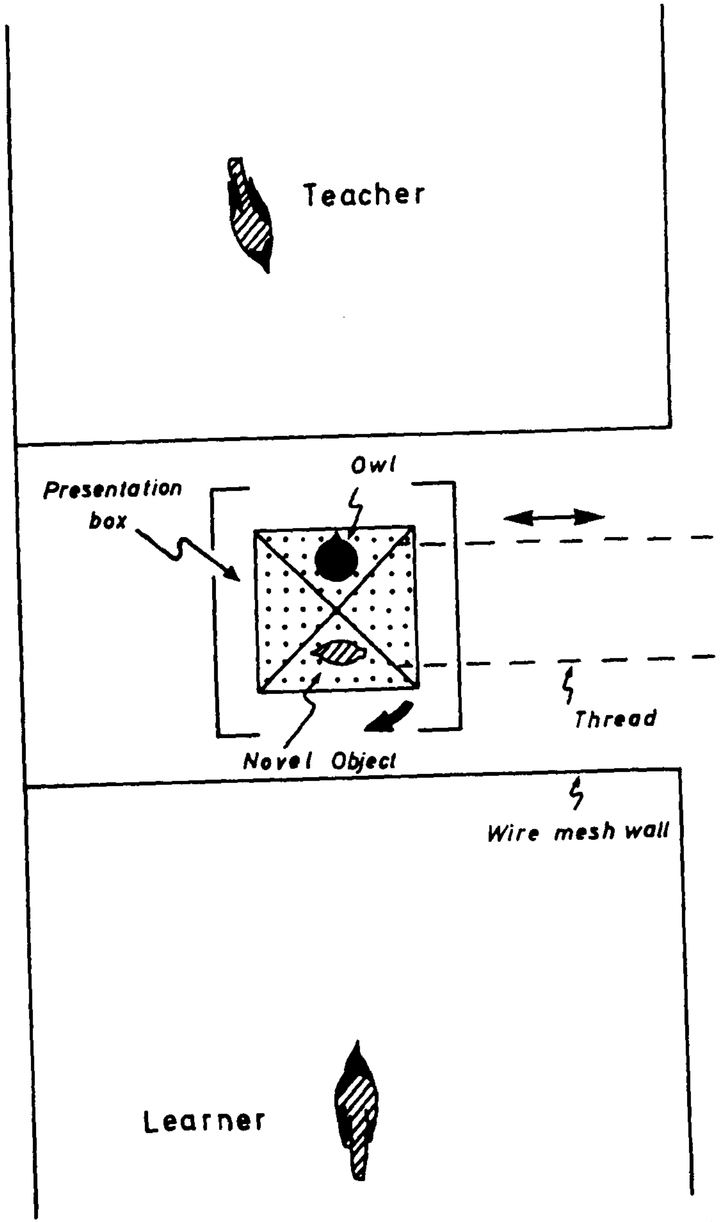

FIG. 12.1 Experimental aviary used to present simultaneously an owl to one blackbird and a harmless songbird or object to another. From "The adaptive significance of avian mobbing. III. Cultural transmission of enemy recognition in blackbirds: Cross-species tutoring and properties of learning", by W. Vieth, E. Curio, and U. Ernst, 1980, *Animal Behavior, 28,* p. 1218. Copyright 1980 by Ballière Tindall. Reprinted with permission.

Choosing a mate: Social effects on choice of partner in guppies

Although evidence of a role for social learning in development of adaptive patterns of response to potential foods and potential predators is now more than 20 years old, comparable evidence of a role of social interaction in mate selection is considerably more recent.

Dugatkin and his co-workers have investigated the role of social learning in mate choice by wild ancestors of a common aquarium fish, the guppy (*Poecilia reticulata*). Guppies were selected for study both because the behavior of members of the species in their natural environment (the streams of Trinidad) would allow social influences on mate selection to occur and because of the ease with which guppies can be bred, maintained, and observed in the laboratory.

In Dugatkin's studies (Dugatkin, 1992; Dugatkin & Godin, 1992, 1993), female guppies serving as subjects first observed two male guppies, one with a female confined nearby and the other without a female companion. The subject females were then given the opportunity to chose between the two males they had just observed when the males were alone. Dugatkin found that females joined the male they had seen courting a female significantly more often than they joined the male they had seen swimming by himself.

Control experiments showed that females were not going to a location where they had seen two fishes in preference to a location where they had seen only a single fish. Nor were females simply approaching a male they had seen engage in courtship; subject females had to see a male actually courting a female (a male courting with no female visible would not do) before they developed a preference for that male.

And, as one might expect, female guppies are not unique in allowing the behavior of other females to influence their choice of a mate. Indeed, copying of the mate choice of others may provide an explanation for some previously unexplained and rather curious phenomena observed in natural settings. For example, in species such as sage grouse (*Centrocerus urophasianus*), in which males compete directly for females on communal breeding grounds (leks), each day a very small number of males enjoy almost all of the access to females. The temporal pattern of copulatory success of different male grouse competing on a lek are consistent with the hypothesis that females observe and copy the mate choice of others, thus producing near unanimity in mate selection on any day (Gibson, Bradbury, & Vehrencamp, 1991).

Perhaps more puzzling has been the observation that male sailfin mollies (*Poecilia latipinna*) regularly mate with female Amazon mollies (*Poecilia formosa*), a gynogenetic species whose members must obtain sperm from male sailfin mollies to produce young, but do not incorporate that sperm into their offspring. Schlupp, Marler, and Ryan (1994) have found that male sailfin mollies that mate with female Amazon mollies gain a reproductive advantage because of the tendency of female sailfin mollies to copy mate choices of Amazon mollies.

There are other ways in which social learning can affect mate choice.

Learning what to sing

It is, of course, impossible to do justice to the immense literature on bird-song learning in a brief review such as the present one. There are, however, several programs of research within that large field that provide evidence that social interactions can direct vocal expression by birds in adaptive directions. I shall review two of the more surprising cases below.

Song learning in cowbirds. It was long thought that song development in males of brood-parasitic species (i.e. species in which females deposit their eggs in the nests of birds of other species and abandon their young for foster parents to rear) was not affected by interaction with conspecifics. However, it is now clear that, like males of other species of song bird, male brown-headed cowbirds (*Molothrus ater*), a brood-parasitic species, learn the fine detail of their songs by interaction with others of their species.

Maintenance of song variants in the repertoires of male cowbirds is determined by responses of females to the songs that males produce. Male songs that, during the breeding season, are most likely to cause female cowbirds to assume the species-typical copulatory posture are responded to by females outside the breeding season with a "wing-stroke" display. After a female responds to a male's song with a wing stroke, the male will repeat the song that elicited the wing stroke several times in succession, thus violating a rule of song production by isolated male cowbirds who normally sing their various song types one after another without repetition.

Those songs that are rewarded by females with wing strokes outside the breeding season are produced by males with greater frequency during the breeding season and increase the probability that the males that sing them will secure copulations (King & West, 1983; West & King, 1988).

The particular form of the songs that male cowbirds sing is further influenced by interactions with conspecific males. Songs that are most effective in eliciting copulatory postures from female cowbirds are also most effective in eliciting attack by cowbird males (West, King, & Eastzer, 1981). Consequently, only dominant male cowbirds can continue to sing the song types most effective in eliciting copulation postures in females (West et al., 1981).

Clearly, social interactions between singers and both male and female members of their audiences determine which elements in the song repertoire of a brow-headed cowbird are most frequently expressed and guide song production in adaptive directions relative to each individual's status within its social group.

Such social shaping of song is particularly interesting because it is one of very few instances in which it is has been convincingly demonstrated that animals actively shape the behavior of conspecifics (for a different view, see Caro & Hauser, 1992).

Tutor tapes, live tutors and song learning in male white-crowned sparrows. Classic studies by Marler (1970) demonstrated that male white-crowned sparrows (*Zenotrichia leucophrys*) readily learn tape-recorded songs. However, such learning from tutor tapes was restricted both to the songs of other white-crowned sparrows and to the first 50 days of life.

Baptista and Petrinovich (1984, 1986) hand reared male white-crowned sparrows for 50 days and then presented them with live (rather than with taped) tutors. Almost all Baptista and Petrinovich's subjects acquired and sang their respective tutors' songs, even though exposure to tutors occurred after the classic, 50-day "sensitive period" for song learning had terminated. Furthermore, songs of live (but not of taped) tutor finches were learned by male white-crowned sparrows, violating the rule, derived from study of responses of male white-crowned sparrows to tutor tapes, that male sparrows will learn to sing only the songs of their own species.

Relatively little is yet known about the aspects of social interaction with live tutors that effect song learning, but in some species, it has been shown that the developing individual will use social cues to select a song model (Payne, 1981). For example, captive Zebra finches (*Taeniopygia guttata*) selectively learned song from the male of a pair that behaved more aggressively towards them (Clayton, 1987).

Conclusion

Exploration of the many ways in which social interaction facilitates acquisition of adaptive patterns of behavior has just begun. We can anticipate further discoveries both of important influences of social learning on the development of behaviors from migration to territoriality and of novel ways in which social interaction shapes and facilitates the acquisition of adaptive patterns of behavior.

IMITATIVE SOCIAL LEARNING

Starting in the late 1890s, and for more than 80 years thereafter, comparative psychologists could not produce convincing experimental evidence that animals could learn by imitation. Consequently, many scientists (myself included) who were interested in whether animals might imitate concluded that they probably could not. The many informal observations suggesting that primates and other animals with relatively large and complex brains spontaneously imitated their keepers (for a review, see Moore, 1992) appeared to be inaccurate, the result of overinterpretation of behavior by scientists observing animals in uncontrolled conditions. However, the last decade has seen a dramatic change in the weight of laboratory evidence concerning the ability of animals to imitate. Indeed today, it is not unreasonable to argue that pigeons, Norway rats and African Grey parrots, as well as chimpanzees and bonobos, can learn by imitation.

During the last decade, there has also been substantial improvement in the quality of observations of imitative behavior in uncontrolled environments that may help to explain earlier failures to demonstrate learning by imitation under controlled conditions as well as some of the recent successes.

Turning anecdotes into observations: Field studies of orangutans

During the 19th century, the study of animal behavior failed as a scientific enterprise, at least in part, because of the willingness of early animal behaviorists to accept at face value anecdotal reports of human-like behaviors of animals (Galef, 1996a). Devastating attacks by Thorndike (1898) and Washburn (1908) on the reliability of informal observation were a necessary first step in the development of a science of animal behavior (Galef, 1996a). Consequently, it is not surprising that the scientific community of the 20th century viewed anecdotal reports of apparent learning by imitation in animals with some skepticism. Only recently has anyone working outside the laboratory attempted to record systematically instances of apparent imitation in a free-living population of animals.

Russon and Galdikas (1993, 1995) used Earthwatch volunteers to observe and record all apparently imitative behaviors spontaneously exhibited by free-ranging orangutans (*Pongo pygmaeus*) at a rehabilitation camp in Borneo where illegally captured animals recovered by the Indonesian government are prepared for life in the wild. Russon and Galdikas (1993) described and recorded on videotape dozens of complex human behaviors that the apes appeared to copy. For example, a worker using a hoe to chop weeds from along the edges of a path placed piles of cut weeds down the center of the path for later collection and disposal. A female orangutan was seen following behind the worker using a foot-long stick and her hands to chop off weeds the worker had missed and piling the weeds she cut in a row down the center of the path.

Although it is, of course, impossible to know just how the apes acquired such behaviors in uncontrolled circumstances, the many instances of copying of complex motor patterns that Russon and Galdikas describe surely suggest that orangutans may be able to imitate under appropriate circumstances. (One must be a little careful here because Russon and Galdikas use the term "imitative behavior" to refer to socially learned behavior sequences, regardless of the behavioral process—e.g. stimulus enhancement, social facilitation, etc.—that may have facilitated their acquisition.) Indeed, Russon and Galdikas's (1995) observations provide some insight into the circumstances that increase the probability of spontaneous imitation by great apes.

Post-hoc analyses of the field observations made in Borneo showed, for example, that a close social relationship between model and mimic increased the probability of spontaneous "imitative behavior". In view of this result, it is, perhaps, not too surprising to find that some of the greatest progress in laboratory studies of imitation of humans by apes have been made using as subjects apes raised in intimate contact with humans.

Affects of "enculturation": Gestural and instrumental imitation by chimpanzees and bonobos

Tomasello, Kruger, and Rutner (1993a) allowed three groups of subjects—(1) human-reared chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) that had been exposed to "language-like" systems of communication (what Tomasello, Savage-Rumbaugh, and Kruger [1993b, p. 1699] called "enculturated chimpanzees"), (2) chimps and bonobos reared by their natural mothers and (3) two-year-old human children—to observe a human model demonstrate 24 different, novel actions performed on objects (for example, placing an object on one's head or using a lever to pry open a paint can). The children were told to *do this*, and the apes had been pretrained to reproduce modeled actions.

The results were clear-cut; apes reared by their natural mothers failed almost totally to imitate the novel actions modeled by an experimenter, whereas two-year-old children and enculturated apes imitated such actions both frequently and equally often.

Custance, Whiten, and Bard (1995) studied development in two nursery-reared chimpanzees of an ability to imitate novel gestures (e.g. lip smacking, finger wiggling, thumb grabbing) demonstrated by human models. Independent observers scoring videotapes of the chimps' behavior were able to identify which of the 48 modeled behaviors the animals were attempting to imitate far more frequently than would be expected by chance.

Last, Whiten and his collaborators (Whiten & Custance, 1996; Whiten, Custance, Gomez, Teixidor, & Bard, 1996) examined imitative behavior in both chimpanzees raised by humans (though not thoroughly "enculturated" in Tomasello et al.'s [1993b] sense of the word) and human infants. All subjects were presented with a transparent plastic box that was held shut by mechanical contrivances that could be opened to obtain a food reward by using either of two techniques, one of which had been demonstrated by a human experimenter. For example, a box could be opened either by pushing or by twisting and pulling on a bolt passing through a pair of rings that held the box closed. After watching a human demonstrator push the bolt to open the box, the chimps were more likely to push than to pull the bolt; after watching a demonstration of pulling and twisting of the bolt, the chimps were more likely to pull than to push it.

In sum, in the last few years, evidence consistent with the view that chimpanzees raised by humans do imitate has been found in one laboratory situation after another. Whether the increased probability of imitation exhibited by apes reared by humans reflects a difference in the attachment of the apes to humans or a more fundamental change in the apes' cognitive abilities remains to be determined.

Imitation in animals other than apes: Norway rats, pigeons and an African Grey parrot

Recent evidence suggests that not only apes, but also other less likely animals are able to reproduce motor acts after observing them. In a series of studies Heyes and colleagues (Heyes & Dawson, 1990; Heyes, Dawson, & Noakes, 1992) allowed observer Norway rats to watch through a wire-mesh partition while a rat demonstrator pushed a joy stick 50 times either to the left or to the right and received a food reward each time that it did so. Once the observer had watched the demonstrator complete 50 displacements of the joy stick in one direction, the observer was placed alone with the joystick and permitted to push the joy stick 50 times, receiving food reward for displacements in either direction. For some groups of observers, the joystick remained in the same position for both demonstration and testing; for other groups of observers, the joystick was moved before testing from near the screen partition that separated demonstrator and observer to the front wall of the chamber (see Fig. 12.2). Under both conditions, the observer showed a reliable tendency to push the joystick in the same direction, relative to its own body axis, as had its demonstrator.

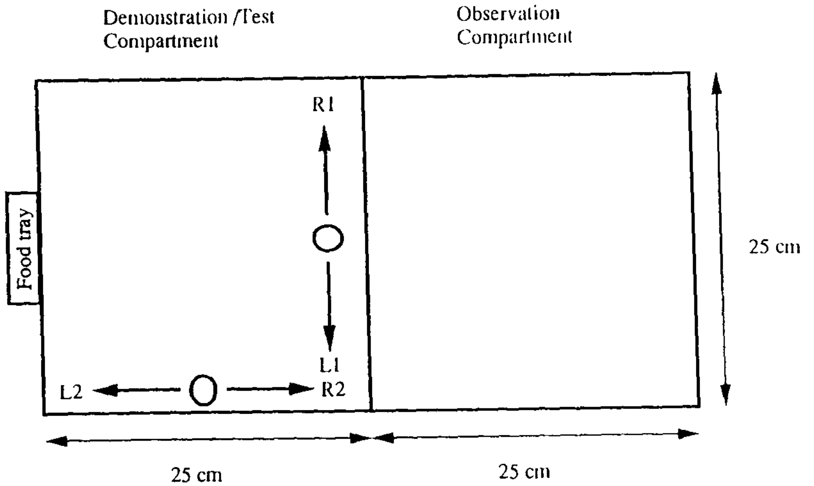

FIG. 12.2 Plan of experimental apparatus showing the position and plane of movement of the joystick during training and testing when the joystick remained in the same position during training and testing (L1, R1) and when it was moved before testing (L2, R2). From "Imitation in rats: Initial responding and transfer evidence", by C. Heyes, G. R. Dawson, and T. Noakes, 1992, *Quarterly Journal of Experimental Psychology, 45B*, p. 83. Copyright 1980 by the Experimental Psychology Society and Lawrence Erlbaum. Reprinted with permission.

Similarly, Zentall, Sutton, and Sherburne (1996) and Akins and Zentall (1996) have reported imitation by pigeons (*Columbia livia*) and Japanese quail (*Coturnix japonica*) of two different motor patterns (pecking and stepping) directed towards a treadle for food reward.

Last, and perhaps most unexpectedly, Moore (1992) has provided evidence of spontaneous imitation by an African Grey parrot (*Psittacus erithacus*). Moore housed the parrot in isolation in a room containing a microphone and video camera that permitted observation of the bird's behavior when it was alone.

Moore visited the bird's aviary several times a day over a period of 5 years. During each visit, he performed repeatedly a small number of movements, each accompanied by a specific word or phrase. For example, as Moore left the parrot's room each day he waved good-bye and repeated the word *ciao*. The bird soon learned to say *ciao* and, by the end of the first year, was observed while alone in its room to say *ciao* and, at the same time, to wave its foot. When in the room with the parrot, Moore would also say *look at my tongue*, open his mouth and stick out his tongue. Some time after it started to wave and say *ciao*, the parrot was observed on television to follow the vocalization *look at my tongue* with mouth opening and tongue raising. The parrot rarely opened its mouth and showed its tongue after saying *ciao* or waved its foot after saying *look at my tongue*.

In all, Moore's parrot was observed to copy 14 different reactions involving six different body parts, associating each with its appropriate verbal label for tens to hundreds of times.

Why the arguing has not ended

An outsider to the field of imitation would probably conclude that, in the face of so much evidence, those interested in imitation learning would have announced the successful demonstration of imitation learning by nonhuman animals and the consequent resolution of a scientific question of long standing. In fact, the announcement has not yet been made. Unfortunately, although almost everyone studying imitation learning in animals now agrees that animal imitation has been demonstrated, there is little agreement as to which experiments demonstrate imitation or even as to which species have been shown to imitate (Byrne & Tomasello, 1995; Heyes, 1995, 1996; Moore, 1996; Tomasello, 1996).

Causes of controversy

Researchers working in different traditions seek evidence of imitation learning in animals for different reasons. Consequently, they use different criteria to identify imitative behavior. Although the criteria researchers use may be appropriate for their respective purposes, without explicit statement of those purposes, disagreement about who has found satisfactory evidence of what is inevitable.

Consider a simple historical example. Edward Thorndike (1898) wanted to know whether, as George Romanes (1884) had proposed, for animals the idea of an act is sufficient instigation to performance of that act. Thorndike (1898) argued if one can from an act witnessed learn to do that act, then clearly the idea of the act is sufficient cause for its execution. Consequently, Thorndike tried to get the cats, monkeys and chickens that he used as subjects in his experiments to imitate very simple actions—in cats, stepping on a treadle or pulling on a string—that are part of their normal behavioral repertoires. Thorndike's repeated failure to find that animals would copy even these very simple acts was one of several pieces of evidence that led him to reject the hypothesis that, in animals at least, the idea of an act suffices for its production.

It should come as no surprise that those working in the tradition of Thorndike (for example, Heyes, 1996, or Zentall et al., 1996) tend to be satisfied with demonstrations that Thorndike was wrong, that animals can, in fact, copy simple actions, and, consequently, that in animals the idea of an act is sufficient to instigate its performance. Such demonstrations of imitation learning are for such researchers, a means to an end, not an end in itself, a starting point for analyses of cognitive processes in the imitating animal.

On the other hand, many contemporary students of imitation learning have adopted Thorpe's (1963) definition of "true imitation" as "the copying of a novel or otherwise improbable act . . ." (p. 135). Thorpe required that the term *imitation* be used to refer only to the copying of unusual actions in order to distinguish imitation from another form of social learning, "local enhancement" ("apparent imitation resulting from directing the animal's attention to a particular object or to a particular part of the environment" [p. 134]) that did not involve the higher mental processes Thorpe felt were involved in true imitation.

Thorpe's reason for requiring that imitation involve copying of complex unusual acts is no longer particularly compelling because in a number of contemporary studies of imitation in animals (e.g. Galef, Manzig, & Field, 1986; Heyes & Dawson, 1990; Whiten et al., 1996; Zentall et al., 1996), discrimination of imitation from local enhancement, social facilitation or other processes has been achieved by requiring not that subjects exhibit a novel behavior, but that they direct two different behaviors towards the same object (Galef, 1988).

On the other hand, those who study imitation in animals because of an interest in the possibility that animals possess human-like cognitive abilities (e.g. Byrne, 1995; Moore, 1996; Russon & Galdikas, 1993; Tomasello et al., 1993a; Whiten, 1996) are, for good reasons, interested in the degree of novelty and complexity of the behavior imitated. If you are interested in similarities in the mental powers of humans and apes (for example, the ability of animals to represent mental states or to understand what others intend [Byrne, 1995]), there is little reason to be interested in studies of the social elicitation of simple skills (like pushing a pole to left or right or pulling vs. pushing a bolt) that are already in an animal's repertoire.

Furthermore, the cumulative culture that supports the biological success of humankind requires an ability to learn complex novel behaviors as a result of observing others exhibit them (Boyd & Richerson, 1996; Tomasello et al., 1993a). Consequently, evidence of an ability to copy faithfully complex, novel behaviors is important to those interested in animal traditions as homologs of human culture (Galef, 1992).

Unfortunately, debating what should or should not be labeled imitation and who has demonstrated imitation in animals has not proved useful. Perhaps attention should be focused instead on the implications of demonstrations of an animal's ability to imitate either novel or familiar acts.

Further difficulties

There is one further problem in using as the sole criterion in studies of imitation either the copying of a novel motor pattern or the directing of two actions toward the same manipulandum. Those interested in behavioral ecology (and I count myself among them) often study imitation in animals not because they wish to understand animal mind or to compare cognitive processes in humans and animals, but because they are interested in how animals acquire patterns of behavior that promote survival and reproduction in natural habitat. For those with an ecological perspective, imitation of meaningless gestures is not nearly so interesting as is imitation of acts that might be instrumental in securing resources that contribute to fitness.

The anecdotal literature has, for decades, provided examples of instances in which captive animals spontaneously reproduce what must be meaningless acts to the animal: Putting on lipstick, blowing smoke rings, limping like a deformed comrade, etc. (for a review, see Moore, 1992). We also now have several laboratory demonstrations of primates or birds (really one bird) copying meaningless gestures they saw demonstrated by humans. What is missing in such examples is any evidence that animals can use their ability to copy motor sequences to learn to solve problems that they might face in the natural world.

Possibility of a solution

Clearly, a demonstration of imitation learning that will satisfy everyone is going to be hard to arrange. It will have to involve comparison of the behavior of observers watching models using one of two different complex, novel motor acts to manipulate the same object in order to secure a reward. The particular motor act used by each observer the first time it manipulates the object will have to match closely that used by its model. Recent work carried out by Whiten and his collaborators (Whiten & Custance, 1996; Whiten et al., 1996) and described earlier, in which "artificial fruits" were opened by chimpanzees using one of two different motor patterns, comes close to satisfying simultaneously all these criteria. There has, however, been some question as to whether the chimpanzees in

Whiten and Custance's (1996) study learned by observation to imitate the specific motor pattern used by their respective models, or simply to either push or to pull the bolt to earn rewards (Tomasello, 1996; Whiten & Custance, 1996; Whiten et al., 1996). Presumably, pushing and pulling were in the chimps' behavioral repertoires before they observed human models opening artificial fruit. Consequently, the imitation may not have been of a novel motor pattern after all.

Still, further development of the technology initiated by Whiten and his co-workers offers hope of demonstration of imitation learning in chimpanzees (or other animals with well-developed manipulative abilities) that all will find satisfactory. Of course, it is always possible that even chimpanzees will lack the ability to imitate when the requirements for imitation are made so severe.

THEORETICAL ANALYSES

The third aspect of the study of social learning that has undergone substantial development during the last decade involves the use of mathematical models similar to those used in population biology, behavioral ecology, and the study of neural networks to explore either the circumstances when it would be advantageous for animals to learn from others or the processes supporting such learning.

The most influential models of social learning in animals build on previous analyses of human culture (Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1981) and extend these earlier models to animal populations (Boyd & Richerson, 1988; Laland, Richerson, & Boyd, 1993, 1996; Rogers, 1988). In general, it is assumed in such models that (1) there are different patterns of costs and benefits associated with individual learning, social learning, and the genetic transmission of information, and (2) natural selection acts on this complex of processes supporting behavioral development to optimize net benefits.

Individual learning is hypothesized to involve potentially costly trial-and-error learning and expensive mental machinery, but to permit rapid response to environmental change. Social learning is considered less expensive to carry out than individual learning, but to involve the risk that the individual one learns from might have acquired its behavior when the environment was in a state different from its current one so that social learning leads to error. Genetically transmitted behavioral propensities are considered cheapest to acquire, but most likely to be maladaptive in changing environments.

Obviously, in such models, the rate of environmental change to which a species is exposed should affect the mix of individual learning, social learning, and genetically transmitted information that species members have evolved to use in developing their individual behavioral repertoires: When environments are essentially constant, all information regarding behavioral development should be transmitted genetically; when environmental change is very rapid, pure individual learning should be favored, and at intermediate rates of environmental change, social learning has the advantage.

In the most widely employed of the current models, the guided-variation model of Boyd and Richerson (1985), it is assumed that individuals acquire behaviors socially by interacting with members of the preceding generation and then modify those socially acquired behaviors on the basis of their personal experience. The social learning part of the process of behavior acquisition can be biased in several ways. For example, naive individuals might have evolved to copy either the most common or rarest behavioral variant exhibited by members of the preceding generation (frequency-dependent bias); naive individuals might copy the behavior of healthy rather than ill elders (indirect bias). Also, transmission of behavior might not be from one generation to the next (vertical transmission) but, instead, proceed from one member of a generation to another (horizontal transmission; Laland et al., 1996). The various models that have been developed to date permit exploration of the conditions under which proclivities for different types of social learning are most likely to evolve.

Because current models of social learning and gene-culture interaction address questions at the population level, they have not told us much about social learning within the individual. Indeed, they were not intended to do so (Laland et al., 1996). The models' creators assume quite simple models of processing at the individual level to make the mathematics of higher-level interactions tractable. Consequently, to date, the impact of theoretical models on experimental work in animal social learning has been somewhat limited. In the longer term, examination at the individual level, of features of social learning important to modeling at the population level (for example, copying fidelity, or probability of copying) should result in empirical work on social learning useful at all levels of analysis.

Attempts are underway to develop models that describe social learning at the individual level. For example, Laland and Bateson are currently using an unsupervised neural-network model to explore the processes needed to support various types of social learning. They have reached the counterintuitive conclusion that imitation learning need not depend on processes fundamentally different from those supporting either individual learning or nonimitative forms of social learning. At the same time, others are developing experimental paradigms that permit direct test of predictions derived from population level theories (Chou & Richerson, 1992; Galef & Allen, 1995; Galef & Whiskin, 1997; Laland & Plotkin, 1990) and analyzing pre-existing data in ways that permit discrimination among different models of the social transmission of behavior through populations (Lefebvre, 1995a,b).

Yet other formal treatments directly reflect the concerns of behavioral ecologists. Giraldeau and his co-workers (Giraldeau, Caraco, & Valone, 1994; Giraldeau & Lefebvre, 1987; Giraldeau & Templeton, 1991) have examined the impact of "scrounging" (exploitation of a resource produced by another), foraging group size, and the complexity of the skills required for food acquisition on the probability of social learning. Barta and Szep (1992, 1995) have examined effects of patterns of food distribution on individual and socal strategies of finding food. Again, the impact of such models on the design and conduct of empirical investigations has been limited (though see Templeton & Giraldeau, 1995). Indeed, one of the more important developments to be anticipated in the study of social learning during the next decade is further integration of experimental and mathematical approaches to the study of social learning.

CONCLUSION

Study of both imitative and nonimitative forms of social learning by animals has made immense strides during the last two decades: (1) The importance of social learning in the development of numerous behaviors affecting survival and reproduction has been clearly demonstrated, (2) there are now a sufficient number of reasonably solid laboratory demonstrations of learning by imitation in animals to convince all but the most skeptical that the phenomenon is real, and (3) theoretical analyses of the role of social learning in the acquisition and propagation of behavior are beginning to influence the design of experiments.

These are exciting times for students of imitation and animal social learning. We are now, after nearly 100 years of effort, in a position to begin to explore the cognitive processes that support imitation learning in various animals and to compare them with similar processes in humans. We have in hand numerous examples of an important role for social learning in the development of biologically important patterns of behavior in animals and analyses of the behavioral processes supporting such social learning. We now have models that permit us to explore the relationships among social learning, individual learning, and environmental factors in the evolution of adaptive response to environmental challenge. A great deal of hard work by scientists in many fields has started to pay off. The next decade of research in the area promises to be at least as productive as the last.

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