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Learning Social Learning

Imitative and Nonimitative Social Learning

Behavioral scientists with an interest in animal social learning have been concerned with one of two quite different issues. Many psychologists and primatologists who study social learning want to know whether animals, other than humans, can imitate, can learn to do an act simply by watching another perform that act.

On the other hand, most biologists who study social learning are more interested in discovering how interaction with others contributes to development of adaptive patterns of behavior in animals living in natural circumstances. Such researchers are usually not too concerned with whether the social learning that facilitates development of adaptive behavior is truly imitative or results from a nonimitative form of social learning.

An animal watching another behave can learn several quite different things. The observer can learn about the behavior of its model, about aspects of the environment that would otherwise be hidden from it, or that the environment can be changed in some way. For example, one chimpanzee might learn from watching another use a stick to pry open a termite mound and eat termites that there is food inside termite mounds. Alternatively, the observing chimpanzee might learn that sticks can be used to break into termite mounds. Or, the observer might learn to insert a stick into a termite mound and apply a prying motion. Only, as in the last case, when the observer learns directly about the behavior of its model, is the learning referred to as *imitative*. Learning about the environment or about possible effects of manipulating the environment is conventionally described as *nonimitative*.

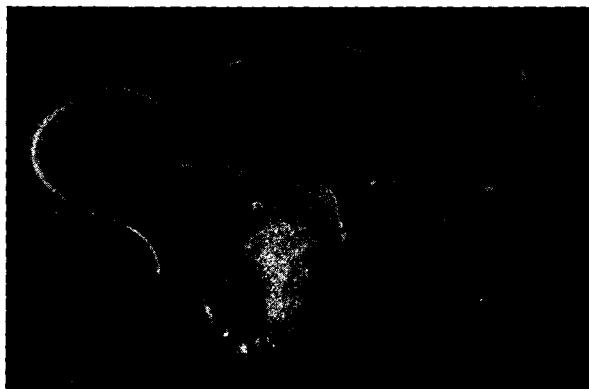
Why is imitation considered special? Because often an observer cannot see its own movements when it imitates the movements of another. For example, if I see you bow and then bow myself, there is no way I can imitate your bow by directly matching what I see when I bow with what I saw when you bowed. Consequently, imitation seems often to require that an observer match signals produced by movement of its own body (*proprioceptive signals*) with representations in memory of visual images of movements made by another. Such *cross-modality matching*, that is, matching proprioceptive signals to visual signals, would seem to require considerable sophistication. It is this potential sophistication in manipulation of representations that has captured the interest of scientists for more than 100 years. There has been considerable progress. For example, structures in the brains of both humans and monkeys have been discovered recently that respond similarly both to seeing an act performed and to performing the act oneself. These *mirror-image neurons*, as they are called, may provide an important first clue as to how imitation is possible.

Nonimitative Social Learning

Nonimitative social learning, which is the focus of this article, is so common in animals and involves so many different types of interaction between a model and a social learner that an entire book devoted to the topic would be needed for a comprehensive review. We have space here to mention only a few examples out of many hundreds of instances of nonimitative social learning now known from the study of animals from insects to primates.

Nonimitative Social Learning in Rats

Following is a detailed discussion of a single example: nonimitative social learning of food preferences in rats (animals often used as subjects in laboratory studies of behavioral development) as a typical case of social nonimitative social learning.



Baby mice suckling off their mother.

© Al Fenn / Time Life Pictures / Getty Images.

Food choices of rats. It is well established that young rats tend to eat the same foods that adult members of their colony have learned to eat, and considerable effort has gone into describing the ways in which interactions between adult rats and their maturing young result in their having similar food preferences. Results of these efforts have revealed a range of social interactions occurring at various stages in development that are important in transmission of food preferences from one generation to the next (*vertical transmission*).

The milk of a nursing mother rat (or human) contains flavors reflecting the taste of the diet she has been eating. These flavor cues allow her suckling young to learn what foods she has been

eating. Young rats choosing their first meals of solid food prefer foods with flavors they have experienced previously in their mother's milk.

When young rats leave the safety of their burrow to seek food in the outside world for the first time, they look for adults, approach them and, if the adults are feeding, eat where the adults are eating in preference to other potential feeding sites. The young often crawl under the body of a feeding adult and emerge right under the adult's chin to eat. So the feeding behavior of young rats can be directed toward specific foods by a feeding adult. Wild rats are hesitant to eat any foods they haven't previously eaten (that is why rats are so difficult to control with poison baits), and once a young rat has been introduced to a food by interaction with adults, many days or weeks may pass before it samples other foods.

As adults eat a food, they mark both the food itself and the area around it with residual chemical cues that are attractive to their young, and young rats prefer marked foods and feeding sites to unmarked alternatives. Further, adults returning from a feeding site to their burrow deposit scent trails leading to the place where they have eaten, and their young will follow such trails from the burrow to food.

Adult rats are also amazingly tolerant of attempts by their young to steal food while the adults are eating it, and young rats subsequently prefer a food they have taken from an adult's mouth to other foods they have eaten.

Last, but not least, after a rat (an observer) interacts with another rat that has recently eaten some food (a demonstrator), the observer has a greatly enhanced preference for whatever food its demonstrator ate. Observer rats smell the food that a demonstrator has eaten on the demonstrator's breath, and experience of the scent of a food together with a chemical produced by the demonstrator causes the observer to have an increased preference for the food that its demonstrator ate. Such socially induced food preferences are very powerful. They can last for weeks, and even cause observer rats that have interacted with a demonstrator rat fed foods laced with pepper (that rats normally avoid eating) to prefer pepper-flavored food.

Social influences of a sort can also determine how rats eat. In much of the world, pine forests are inhabited by squirrels that live on pine seeds that they remove from the pinecones.

that grow everywhere in the forest. However, there are no squirrels in Israel, and rats living there have occupied the ecological niche that squirrels fill elsewhere.

Extracting pine seeds from pinecones is not easy for rats. To recover more energy from the pine seeds than is used to extract them from under the tough, non-nutritious scales that protect them, rats must use a rather special technique that takes advantage of the structure of pinecones. The scales surrounding the base of a cone must first be removed. Then, the spiral of scales that circle the pinecone's shaft from its base to its tip must be removed one after another in sequence.

Studies in captivity of several hundred rats taken from areas in Israel other than pine forests revealed that only a handful ever learned for themselves to use the spiral pattern of scale removal that permits a rat to maintain itself on a diet of pine seeds and water. Most rats taken from outside of pine forests either ignored pinecones or gnawed on them in ways that produced few seeds in return for much work.

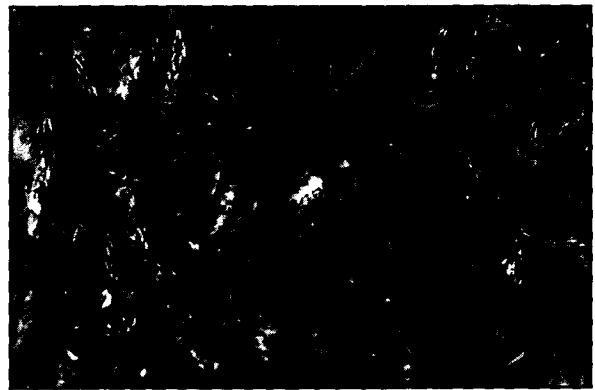
On the other hand, all rats captured in pine forests knew how to extract seeds from pinecones efficiently, and so did rats that were taken as infants from mothers living outside pine forests and given to mothers who knew how to open pine cones and were living on a diet of pine cones and water. Further studies revealed that young rats allowed to finish stripping scales from pinecones started appropriately by an adult rat became efficient exploiters of pinecones, and so did young rats given pinecones a human had stripped of scales, mimicking the early stages of scale removal used by successful adult rats.

Social learning by rats of the efficient method of opening pinecones is particularly interesting because here social learning opened a new ecological niche to a species, allowing rats to thrive in a portion of the environment that was otherwise closed to them.

More Examples of Nonimitative Social Learning

As we have seen, rats can learn socially by nonimitative means what to eat, where to eat, and how to eat difficult foods. Of course, animals other than rats also use nonimitative social learning to increase the efficiency with which they learn to exploit resources. Perhaps surprisingly, honeybees are among the most sophisticated social learners on our planet. Like the rats discussed above, honeybees have several ways to communicate about foods. A successful forager that has returned to its hive with a load of nectar performs a dance on the honeycomb within the hive. The dance provides fellow foragers with information as to the direction and distance to the place where the returning forager has gotten the nectar it is carrying as well as its sugar content. Bees also mark rich food sources with a scent that is attractive to their fellows and carry food odors back to the hive on their bodies that other foragers can use to identify the place where the returning forager has been feeding.

Birds can use the behavior of others not only to locate potentially profitable places to feed and to select appropriate items to ingest, but also to decide when food in an area has been exhausted, and it is time to move on to forage. Fish



A bee with a number attached to it "dances" to communicate a feeder location to other members of the swarm during an experiment at Michigan State University.

© James L. Amos / Corbis.

also often feed socially, as do insect-eating bats, though relatively little is known of the details of their social feeding.

Animals learn about many things other than food by interacting with their fellows. Naive young monkeys, blackbirds and kangaroos have been shown to learn to identify potential predators by watching the responses of knowledgeable individuals to potentially dangerous objects. Both female birds and female fish learn about the desirability of potential mates by watching other females of their species choose a partner, and male birds and fish can appraise the fighting ability of potential opponents by "eavesdropping" on them while they engage in aggressive interactions with others.

The list of behaviors that have been demonstrated to result from nonimitative social learning is long and growing. And, as anyone who regularly watches nature shows on television surely knows, the list of behaviors of animals—from chimpanzees, using twigs to fish for termites, to dolphins, holding sponges in their mouths while feeding—that might be acquired by interaction with others is even longer.

Why Learn Socially?

There are three ways that animals can develop adaptive behavioral repertoires. First, their behavioral development may be highly constrained so that behaviors that are typical of a species (i.e., instincts) develop in essentially any environment. Second, an individual may learn to behave appropriately from trial-and-error interactions with its physical environment, and third, an animal may learn socially, through interaction with others of its species.

Within an individual's life span, instincts cannot change in response to changing conditions. Trial-and-error learning can track environmental changes, but is relatively time-consuming, and as its name implies, involves making mistakes that may be life threatening. An animal whose individual learning about the environment is biased by interaction with others of its species enjoys the best of two worlds. Such an animal can respond adaptively to the environment in which it matures without incurring all the costs associated with learning independently about what works and what doesn't work. Learning by interacting with more knowledgeable others should be advantageous in many circumstances.

Learning by imitation appears to require neuronal systems that are probably expensive both to construct and to maintain. Consequently, animals that can learn socially by nonimitative means may be able to realize the benefits of social learning without incurring costs associated with building and maintaining a nervous system able to learning by imitation.

See also Behavioral Plasticity

Communication—*Honeybee Dance Language*

Learning—*Insight*

Learning—*Social Learning and Intelligence in Primates*

Social Organization—*Social Knowledge in Wild Bonnet Macaques*

Further Resources

Galef, B. G., Jr. 1996. *Social influences on food preferences and feeding behaviors of vertebrates*. In: *Why We Eat What We Eat* (Ed. by E. D. Capaldi), pp. 207–231. Washington, D.C.: American Psychological Association.

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- Heyes, C. M. & Galef, B. G., Jr. 1996. *Social Learning in Animals: The Roots of Culture*. San Diego, CA: Academic Press.
- Seeley, T. D. 1995. *The Wisdom of the Hive*. Cambridge, MA: Harvard University Press.
- Zentall, T. R. & Galef, B. G., Jr. 1988. *Social Learning: Biological and Psychological Perspectives*. Hillsdale, NJ: Lawrence Erlbaum Associates.

Bennett G. Galef, Jr.

■ Learning

Social Learning and Intelligence in Primates

Our quest to understand human origins encompasses a long-standing interest in the roots of human intelligence. Humans are set apart from other animals for their high level of cognitive functioning, particularly evident in their dealings with their social world. Notably, humans are specialized in forging and handling complex social relationships, predicting and manipulating the behavior of others, and maintaining social balance and group cohesion. In addition, humans have perfected means of communicating about themselves and others (i.e., by using language). Lastly, humans form mental representations of themselves and others, and are able to reflect on their own mental states (e.g., desires, fears) as well as those of others (i.e., through mind reading and empathy). To better understand the evolution of human cognition, anthropologists have adopted the classic comparative approach, turning their attention to the cognitive skills of other anthropoid primates, such as monkeys and apes. By relating the variation in mental abilities present across species to generalized patterns of morphology, ecology, or behavior, primatologists have formulated several hypotheses to account for the seemingly exceptional cognitive abilities of primates. This discussion presents the major candidates, focusing on the *Social Intelligence Hypothesis*, which postulates that cognition evolved in response to the demands imposed by the animal's social environment.

Despite surprisingly little evidence to support the assumption that cognitive capacities and brain size are linked, primate intelligence traditionally has been attributed to a relatively large brain. The degree of "encephalization" (the proportional size of the brain relative to some other body measure) provides a gauge of the expected brain size for any given body size, and primate quotients exceed those predicted for their body size. More specifically, primate cognitive capacities have been ascribed to structural reorganization of the brain, for instance, through greater investment by anthropoid primates in the visual system (as opposed to the olfactory system). Some researchers also have proposed that human cognition and language result from delayed maturation of the brain; however, the comparably slow developmental trajectory of newborn great apes suggests that the extent of human brain immaturity at birth and subsequent developmental delay has been exaggerated. Nevertheless, if factors such as brain size or organization account for human intelligence, it still leaves open the question of why these changes in the brain occurred.

Because increasing brain size also correlates positively with certain life history variables, such as an extended period of infant dependency, delayed sexual maturity (or increased juvenility), and longevity, other theorists have proposed that primates can achieve greater cognitive feats because of their slower progression through longer life stages. In other words, young animals have more supervised time at the bosom of their social group and under the tutelage of older family members, which provides the necessary circumstances for them to learn difficult skills.