

Social Learning in Animals

Intermediate article

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'Social learning' is a general term referring to several behavioral processes that allow social interactions to bias what individuals learn. Processes involved in social learning include 'local enhancement', when the normal activities of one individual simply focus attention of others on a particular part of the environment with which they then interact, and 'teaching', when a model changes its own behavior to facilitate learning by naive individuals.

INTRODUCTION

Understanding the behavioral processes that promote diffusion of behavioral traditions through animal populations, and comparing these processes with those that support culture in human societies, suggests important similarities as well as important differences in the processes that support social learning in humans and animals. This article discusses a variety of such social learning processes that are common to both humans and animals, and two of these processes, namely imitation and teaching, that may be used only by humans and their closest relatives.

WHAT IS SOCIAL LEARNING?

Understanding the role of behavior in promoting survival and reproduction is a goal of life scientists working in a variety of disciplines. Students of animal social learning are particularly interested in the question of how interactions among members of a species affect development of their behavioral repertoires. Social learning is only one of several factors that interact to influence behavioral development. For example, ethologists studied instinctive patterns of behavior produced by natural selection acting on heritable variation, whereas students of animal learning were and are interested in how individual experience of events in the physical environment shapes behavior.

EXAMPLES OF SOCIAL LEARNING

Contemporary interest in social learning arose from the observation that members of one free-living population of a species often behaved quite differently to members of other populations of the same species. For example, chimpanzees living to the west, but not to the east, of the Sassandra-N'Zo river on the Ivory Coast use stones to crack nuts (Whiten *et al.*, 1999). Of course, population-specific behaviors such as nut cracking could reflect differences in either the genetic substrate of populations (i.e., different subspecies of chimpanzee might inhabit the two banks of the Sassandra-N'Zo river) or differences in the physical environments in which the two populations live (e.g., there might be no nuts on the east bank of the river). In fact, there are no known genetic differences between chimpanzees on the two banks of the Sassandra-N'Zo, and similar nuts and stones are found in both places.

The nut-cracking example is not unique. There are often systematic differences in the behavior of populations of a species even when there is no evidence of genetic or environmental differences between populations (Whiten *et al.*, 1999). For example, chimpanzees living in Gombe National Park in Tanzania use twigs or blades of grass to feed on ants and termites. These implements are used to probe the passageways of insect mounds, and when the residents attack an intruding probe, the chimpanzees extract the probe and eat any termites that are clinging to it.

There is variation among chimpanzee populations not only in the species of insect preyed upon and the materials used as probes, but also in how probes are prepared for fishing and how insects are captured. For example, chimps at Gombe in Tanzania hold a long stick in one hand and use the other hand to wipe a ball of ants into their mouths. Chimps living in the Tai Forest on the Ivory Coast use a short stick to collect ants, and they place the

stick directly into their mouths, removing the ants with their lips and tongue. Chimpanzees at Assirik in Senegal usually peel bark from twigs before using them as probes, whereas chimpanzees at Gombe do not peel the twigs before using them. Such observations have led many scientists to conclude that at least some population-specific behaviors of chimpanzees are traditions learned by one individual as a result of observing the behavior of another individual (McGrew, 1992; Whiten *et al.*, 1999).

It has been known for many years that some animals can learn complex patterns of behavior by imitating others of their species. 'Imitation' is a special type of social learning that has been defined in different ways by different scientists. For example, imitation has been defined both as 'copying of a novel or otherwise improbable act' (Thorpe, 1956) and as 'learning to do an act from seeing it done' (Thorndike, 1898). An example of the former is to be found in the songs that adult male songbirds produce both to attract conspecific females and to repel conspecific males. Males from different populations of many species produce different variants of a basic, species-typical song, and laboratory studies have shown that a 'song dialect' is produced only by males that, as juveniles, heard adults of their species sing that dialect (Marler, 1970).

Thus we know both that even birds (with their relatively small brains) can learn song dialects by imitation, and that chimpanzees from different populations engage in different feeding behaviors. Why should we not simply conclude that if a difference in the behavior of two groups of chimpanzees cannot be explained easily by reference to differences in either their genes or their ecology, the different behaviors have been transmitted by imitation among chimpanzees within each group?

Although birds learn their songs by imitation, as we shall see below, this may be a special case. More often, when a possible instance of learning by imitation observed in natural circumstances is brought into the behavioral laboratory for analysis, it is found that the learning depends on some social learning process that is not truly imitative. For example, rats living in the pine forests of Israel are unique in that they, and no other rats, survive by stripping the scales from pine cones and eating the pine seeds that the scales protect (Aisner and Terkel, 1992). It is difficult for rats to strip pine-cones in a way that allows them to get more energy from the pine seeds than is consumed in obtaining them. The rats must start by removing the scales from the base of a cone, and then take advantage of the cone's architecture by removing the remaining

scales in a spiral from the base of the cone to its apex. A more direct method, which involves gnawing through individual scales to access seeds, is used by rats from populations that do not typically feed on pine-cones if given access to them. However, this method consumes more energy than it produces.

In the laboratory, rats born to pine-cone-stripping mothers grew to strip pine-cones in the efficient manner only if they were reared by adult rats that demonstrated pine-cone stripping, and not if they were foster-reared by adult rats that did not know how to open cones efficiently. Furthermore, even young rats reared by adults that did not know how to strip pine-cones became efficient strippers of seeds when provided with cones started appropriately by either an adult rat, or a human using a pair of pliers to remove scales from the base of the cones. Apparently, interaction with cones started in the right way guides the development of behavior in young black rats, making them efficient strippers of seeds from pine-cones. In nature, young rats probably snatch partially opened cones from adults, and by interacting with the cones learn how to finish the job.

The study of social learning in Israeli rats has yielded two important findings. First, complex motor patterns can be transmitted from one generation of animals to another. Second, the existence of a complex tradition of behavior in a population of animals cannot be used to infer that a complex social learning process, such as imitation or teaching, was involved in its transmission.

CLASSIFYING SOCIAL LEARNING

Some authors have suggested that describing a behavior as traditional is totally uninformative unless the spread of the behavior through a population can be attributed to a particular social learning process. This is almost certainly an overstatement. Referring to a behavior as traditional implies that the spread of that behavior through a population was facilitated by social interactions (i.e., that each group member did not learn the behavior independently). Still, the assertion that describing a behavior as traditional is uninformative raises an important issue. As we have already seen in the cases of bird-song learning and pine-cone stripping, animals may influence one another's behavior in quite different ways. Consequently, for those with an interest in understanding how behaviors develop, describing a population-specific behavior as traditional answers relatively few questions and raises many.

While almost everyone seems to find instances of traditional behavior in animals intrinsically interesting, many outsiders to the field of social learning find attempts to categorize the many ways in which social interactions affect the acquisition of behavior either boring or impenetrable. Admittedly, attempts to define various social learning processes have produced quite complex and not altogether satisfactory vocabularies describing the many ways in which social interactions can bias behavioral development (Whiten and Ham, 1992). However, such attempts at categorization are important because they make explicit the fact that social learning can occur in many different ways in both humans and other animals.

One rather simple way in which one animal can bias development of the behavior of others, thereby facilitating spread of the behavior through a population, is by focusing the attention of others on particular parts of the environment. For example, if one Norway rat sees others eating in a particular place, or smells rat odors left at a potential feeding site by other rats that have eaten there, that rat is much more likely to begin eating whatever food is at the socially marked site than to start eating at unmarked sites where different foods might be available. Because wild Norway rats are extremely reluctant to eat unfamiliar foods, anything that causes a rat to begin eating one food rather than another has a profound effect on the rat's subsequent food choices.

Such social biasing of learning by other individuals has been termed 'local enhancement', defined as 'apparent imitation resulting from directing the animal's attention to a particular object or to a particular part of the environment' (Thorpe, 1956). Local enhancement can be contrasted with imitation, defined as 'copying of a novel or otherwise improbable act' (Thorpe, 1956) or 'learning to do an act through seeing it done' (Thorndike, 1898).

In local enhancement, an animal learns only that it should interact with one part of the environment rather than with another. In true imitation, an animal learns directly about the behavior in which it should engage. The distinction is fundamental to all academic discussions of social learning in animals.

Are two terms – local enhancement and imitation – sufficient to enable discussion of all animal social learning? Unfortunately this is not the case. Humans and other animals can learn from the behavior of others, either directly or indirectly, in more than one way. For example, if a chimpanzee watches another of its species use a rake to pull in food items that would otherwise be out of reach,

the observing chimp learns to use the rake to pull in food faster than it would if it had never seen another chimp use a rake (Tomasello *et al.*, 1987). However, observer chimps failed to imitate in the sense of copying the particular actions used by the demonstrator to obtain food. Rather, observers developed their own techniques for using the rake. Observers seemed to learn that a rake was useful for acquiring food, but did not learn much about the actual behavior that a model uses when raking and, as noted above, what is meant by imitation is 'learning to do an act'. Tomasello *et al.* (1987) proposed that the observers were not so much copying the model's behavior as attempting to create the results of the model's efforts, a process that they termed 'emulation.'

Finally, consider teaching, an activity which contributes to social learning and that is common in our own species. In local enhancement, imitation or emulation, the model is essentially passive. The observer extracts information from a model engaged in activities it performs without reference to the observer. In teaching, according to the most widely used current definition (Caro and Hauser, 1992), a model modifies its behavior in the presence of a pupil, often leading to some reduction in the efficiency of the model's performance. Furthermore, the model either encourages or punishes the pupil, or provides the pupil with examples of behavior or experiences so that the pupil acquires information or skill more rapidly than it otherwise would.

The important elements of this somewhat complex definition, distinguishing teaching from other activities that play a part in social learning, involve potentially costly modification of the teacher's normal behavior, resulting in accelerated learning by pupils. Surprisingly, given the importance of teaching (at least in modern Western societies), there are few plausible examples of teaching in the animal world, and even those few instances are hotly debated. Feline mothers may meet the definition by delaying their killing and eating of prey and providing their young with incapacitated, live prey on which to practice predatory behavior. However, there is contradictory evidence as to whether experience with incapacitated prey facilitates the development of hunting behavior in young cats. Some authors have suggested that killer whales teach their young to hunt seals, although this view is not generally accepted (Rendell and Whitehead, 2001). Chimpanzees may teach juveniles how to crack open nuts using a stone hammer and anvil (Boesch, 1991).

It is worth quoting verbatim Boesch's (1991) descriptions of one such instance, as they provide

a fine indication of both the strengths and the weaknesses of unusual field observations. Ricci's 5-year-old daughter Nina is trying without success to crack open nuts using an irregularly shaped hammer. Ricci joins Nina, and Nina gives the hammer to Ricci.

Then with Nina seated in front of her, Ricci, in a very deliberate manner, slowly rotated the hammer into the best position with which to pound the nut effectively. As if to emphasize the meaning of this movement, it took a full minute to perform this simple rotation. (Boesch, 1991, p. 532)

Ricci then cracks 10 nuts with the hammer in the correct position, and leaves. Nina then picks up the hammer, adopts the same grip that her mother used to crack nuts successfully, and she opens four nuts in 15 minutes. According to Boesch:

In this example, the mother corrected an error in her daughter's behaviour and Nina seemingly understood this perfectly, since she continued to maintain the grip demonstrated to her. (Boesch, 1991, p. 532)

Some authors accept Boesch's interpretation of his observations, while others do not. The fact that such complex interactions between an apparent pupil and teacher have been seen only twice in many years of field study surely makes them difficult to interpret with certainty. Indeed the issue of whether animals teach is only one of a number of questions that are being actively debated by researchers who are interested in social learning in animals.

DISPUTES ABOUT SOCIAL LEARNING

For more than a century, two central questions have motivated much of the research on social learning in animals.

1. Which non-human animals, if any, imitate?
2. What is imitation and how can it best be distinguished empirically from other forms of social learning, such as local enhancement?

Can Animals Imitate?

The discovery over decades that many different types of social learning can bias behavioral development has made it increasingly difficult to determine whether any given case of social learning is a product of true imitation or of some other less cognitively demanding process. Why should anyone care enough about the types of social learning that animals employ when using one another as sources of information about the environment to actually argue about it? Many believe that

understanding similarities and differences in social learning processes in humans and other animals will provide insight into similarities and differences in their mental processes. Indeed, the first laboratory investigations of social learning in animals were undertaken in order to determine whether, like humans, non-human animals had access to mental representations that they could manipulate in order to solve problems (Thorndike, 1898).

To imitate the behavior of a model, an imitator must store a visual image of the model's behavior and then match its motor output to that stored representation. Earlier we considered the learning by birds of song dialect as a result of hearing the song of adults belonging to their social group. Such learning might be described as 'learning to sing a song from hearing it sung'. This is somewhat different from 'learning to do an act from seeing it done', which some hold to be the definition of imitation.

Why should a distinction be made between seeing and hearing when defining imitation? The task of learning to sing a song by listening may be far simpler than that of learning to do an act by seeing it. In order to learn to sing like another, all the singer needs to do is to match the sounds it produces when singing with a stored representation of the sound of the song of another. Thus song imitation can occur within a single modality, namely audition. On the other hand, when learning to perform an act by seeing it done, a match has to be made across modalities, between a stored representation of a visual stimulus (the sight of another performing a behavior) and kinesthetic feedback from a motor act. Such cross-modality matching is necessary because even if an observer perfectly imitates an act performed by a model, the visual input to the observer while imitating is quite different to the visual input that the observer received when observing the model perform the act. For example, when I see someone bow, what I see is very different from what I see when I bow myself. On the other hand, when I whistle a song, what I hear is very similar to what I heard when someone else whistled the same song (Heyes, 2001). So when we are discussing imitation in animals, should we be limited to instances where overt motor patterns are copied, or should we include bird-song learning? Most authors think that we should not include bird-song learning.

There is even controversy about whether, in order for a behavior to be considered a result of imitation, the imitated behavior has to be new to the imitator and, if so, how one knows whether a motor pattern is really new. With regard to the first

point, how can you tell if an individual has learned to perform an act by seeing it done, if it has previously performed the act? With regard to the second, an individual may never have used a rake to pull in food before, but it has grasped objects, used objects to move other objects about, sought food, etc. An apparently novel act may be nothing more than a combination of acts that are already in an individual's repertoire. Perhaps all a subject does when it imitates a familiar act is to use the behavior of another as a cue as to which elements of its own behavioral repertoire it should try in the situation that it now faces. If you are interested in imitation as a tool for exploring the cognitive capacities of animals, then cases in which observers simply use others' actions to cue their own behavior are not very informative.

What is the Best Empirical Method for Discovering Imitation?

For many decades the predominant strategy for demonstrating imitation learning was first to determine whether watching the performance of a task allowed observers to learn to perform that task faster than animals that did not have the observational experience, and then by conducting additional experiments, to attempt to exclude all explanations of the accelerated performance other than imitation. As the number of alternative social learning processes described by scientists increased, the strategy of excluding alternatives became increasingly cumbersome. For example, if kittens are allowed to watch a demonstrator cat press a lever to obtain food, they subsequently learn to press the lever faster than kittens that do not see a cat receiving rewards for pressing the lever. To determine whether this accelerated acquisition of lever pressing was due to imitation of the cat by the kittens, one would have to exclude, among other things, the possibility that lever pressing is facilitated by either local enhancement of the lever or observing others eat. In general, such attempts have produced no convincing evidence of imitation learning in any animal.

At present, the 'two-action method' is the preferred laboratory procedure for discovering imitation in animals. In the two-action method, each subject sees a demonstrator receive rewards for manipulating an object in one of two ways. The observer is then given access to the object, and it is determined whether observers tend to manipulate the object in the same way as the demonstrator did. For example, chimpanzees first watch a human demonstrator either pull or twist bolts in

order to open a closed box containing fruit, and they are then given a closed box. The most recent evidence suggests that chimpanzees tend to use the same action that they saw demonstrated to open the box (Whiten, 1998). Surprisingly, the two-action method has also produced evidence of apparent imitation in Japanese quail, starlings, pigeons, grackles, and budgies (Heyes, 2001), although other methods for demonstrating imitation have not provided evidence of the latter, even in animals as sophisticated as monkeys (Visalberghi and Fragaszy, 2002).

Perhaps more fundamentally, there is even a question as to whether evidence gathered in the field or evidence collected in the laboratory is more suitable for determining whether members of a species can imitate. Laboratory workers feel that the social learning mechanisms responsible for apparent imitation of one animal by another can be analyzed satisfactorily only in the controlled environment of the laboratory. However, some field workers suggest that the sterile environment and abnormal social conditions of the laboratory result in systematic underestimation of the imitative abilities of complex animals such as chimpanzees (McGrew, 1992).

Just How Important is Social Learning to Animals?

Recently, several students of animal behavior have argued in book-length monographs that social learning is central to the development of adaptive behavioral repertoires in a variety of animals (Avtal and Jablonka, 2000; Dugatkin, 2000). These authors argue that social learning and natural selection are practically co-equals in producing adaptive behavior in animals, and that social learning of one type or another is necessary for animals to maximize everything from selection of a mate to avoidance of potential predators. Although social learning has been demonstrated to play some role in the mate choices of guppies and quail, and in the avoidance of predators by blackbirds and monkeys, claims of a major role for social learning in the evolution of behavior are relatively recent, and have yet to be evaluated. Still, the issue of just how important social learning is to understanding animal behavior is an open one, and is sure to be contentious.

THE ROOTS OF CULTURE

An intense area of debate concerns the degree of similarity between 'traditions' of animals and

'cultures' of humans. As is often the case in discussions of the relationship between human and non-human animals, some authors emphasize apparent similarities and others highlight apparent differences. The former group suggests, for example, that if an anthropologist were to describe populations of humans whose technologies and social customs varied as much as do those of well-studied populations of free-living chimpanzees (Whiten *et al.*, 1999), the anthropologist would surely refer to the human populations as having different cultures. Therefore it is foolish to deny culture to chimpanzees (McGrew, 1992).

Those in the opposing camp look at the same data and focus on apparent differences between chimpanzee and human social learning. They argue that differences in the behavioral repertoires of various groups of chimpanzees tell us nothing about the processes responsible for the development of those differences. Moreover, if you are interested in discovering true precursors of human culture, you should look for behaviors that are transmitted from one generation to the next by the same processes that support human cultures (Galef, 1992). Humans can teach one another; they do learn by imitation. As we have seen, generally animals do not teach, and they rarely learn by imitation. Consequently, most instances of human culture and animal tradition may depend on rather different behavioral processes.

The type of culture that animals which do not teach or imitate could produce would be severely restricted. In human cultures, techniques or behaviors often become increasingly complex over generations. Youngsters learn from elders what the elders know. The young can then spend a lifetime improving on what they have learned socially, and then transmit those improvements as the starting point for the next generation. Such 'ratcheting' can occur only if social transmission involves learning directly about behavior, as in imitation or teaching, not when social transmission involves changes in attention to environmental stimuli, as in local enhancement or emulation.

A local enhancer only increases attention to some aspect of the environment. A model for emulation merely indicates that a tool can be used to achieve a goal. Consequently, in each generation, naive individuals whose learning was shaped by local enhancement or emulation must learn for themselves how to behave with respect to the part of the environment to which their attention was directed, and no ratcheting across generations can occur.

The argument goes on. Many, perhaps the majority, of those who study apes in their natural

environments are convinced that these animals exhibit something quite similar to human culture. Many, perhaps the majority, of those who study social learning processes in animals in the laboratory believe that the differences between human culture and animal tradition are sufficiently great to require different terms to describe them. They often want to restrict use of the term 'culture' to humans, and to refer to 'animal traditions' when discussing population-specific behaviors of non-human animals.

Is There Anything Worth Arguing About?

At first glance, such arguments over terminology may seem arcane or even useless. However, our language both reflects and influences the way in which we think about the natural world. Those who believe that it is appropriate to discuss 'culture' in animals generally differ from those who prefer to talk about 'animal traditions' in their views of how similar the behavioral and mental capacities of human and non-human animals may be.

Understanding how we humans both resemble and differ from other animals is neither arcane nor useless. It is a basic part of our effort to discover what we are as a species, and to define the ways (if any) in which we are unique among animals. Thus unraveling the processes involved in social learning in animals, whether they are living free in their natural habitat or maintained in the more restricted laboratory environment, is but one of many ways available to us to increase our understanding both of ourselves and of our place in nature.

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