Animal Intelligence

Insights into the Animal Mind

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Tradition and Social Learning in Animals

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Tradition and social learning are intimately related because the capacity for social learning is a prerequisite for the establishment and maintenance of true traditions in a population. Although tradition and social learning are clearly linked to one another, the methods appropriate for the study of each are quite different.

A tradition is a learned pattern of behavior that is common in a particular social group, but absent in other social groups of the same species. The existence of a tradition can be identified by careful, unobtrusive observation of organisms in undisturbed environments. The term "social learning," on the other hand, refers to a class of behavioral mechanisms that may result in the production of a tradition in a population. Such mechanisms can be analyzed only by experimentation under controlled conditions.

The reason why this distinction between tradition and social learning is important is that observation of a tradition in a population of animals has frequently been used to infer the existence of a complex social learning process underlying that tradition. I intend to show that such inferences are not justified, and that traditions may be established and maintained in populations by quite simple types of social learning. The existence of traditions in a species is not necessarily evidence of an ability of members of that species to learn by imitation, observation, or in any other sophisticated way. For example, it has been well established by observation that many species of British birds have acquired the habit of opening milk bottles and eating the cream from the milk's surface (Fisher and Hinde 1949).

Description of the spread of this habit among birds in several areas strongly suggests that social interaction is important in propagation of the behavior. But is it the case that one bird learns to open milk bottles by watching another bird do so? It is perhaps at least as likely that after one bird has opened a milk bottle, others come to feed from the opened container and are themselves subsequently more likely to attempt to feed at closed bottles. The existence of a tradition of feeding from milk bottles is well established, but it is not clear what inferences concerning the learning capacities of birds should be drawn from the existence of that tradition.

A Brief History of the Study of Animal Traditions and Social Learning

The possibility that traditions may rest on rather humble foundations was first suggested more than 70 years ago by Edward Thorndike (1911), the founder of North American animal experimental psychology. However, Thorndike's approach to the analysis of social learning has not as yet, at least not in many popular texts, replaced the view prevalent in the late nineteenth century that traditions are indications of considerable mental sophistication in their bearers. It is worthwhile to recount some of the relevant history of the issues involved in order to clarify some of the confusion that still exists today.

In the decades before comparative psychology or the study of animal behavior from a biological perspective became experimental disciplines, it was commonly believed by naturalists, pet owners, animal trainers, and others familiar with animals that mammals generally could learn to perform complex acts by observing and then imitating others performing those acts. There was no compelling evidence of learning by observation or imitation in animals; belief in such processes was just one of a number of widely held but unexamined notions about animal functioning common during the Victorian era.

The question of whether animals would, in fact, learn by observation became theoretically important at the close of the nineteenth century as the result of a fundamental disagreement between the co-originators of evolutionary theory, Alfred Russel Wallace and Charles Darwin. Though Wallace and Darwin agreed about many things, they differed fundamentally over the origins of the human mind. Darwin was convinced that the human mind, like other features of living organisms, was the product of purely natural processes. Wallace argued that natural processes alone were insufficient to produce the intellectual sophistication of mankind. Thus, in the 1880s, when the question of the applicability of evolutionary models to understanding of human functioning was actively debated (as it is today in a different context), the question of whether animals had faculties of mind similar to those found in man was of importance. If one could identify simplified precursors of human intellectual capacities in animals, then continuity from animal to man in intellectual life would be established and there would be no need to invoke extra-natural causes in discussing the origins of human mental functioning. If, to the contrary, man had intellectual capacities for which no simpler precursors could be found in nonhuman animals, then an evolutionary explanation of the human mind would be more difficult to maintain.

The major contributor of evidence to the Wallace-Darwin controversy was Darwin's protégé and disciple, George Romanes, a Fellow of the prestigious Royal Society and a leading figure in the biological establishment of his day. Romanes's approach to the problem of determining whether there was continuity in the intellectual capacities of animals and man was to postulate a hierarchy of mental faculties (Romanes 1882, 1884). This linear scale of qualities of mind extended from the protozoa, which it was said exhibited only excitability, conductility, and the capacity to discriminate among stimuli, to modern Western man, the possessor of the faculties of reason, conscience, and abstraction in their highest states of development. Using such a scale one could, at least in principle, rank-order species by their capacity to exhibit the mental faculties most clearly shown by humans.

Imitation was an important mental faculty for Romanes's (1884) analysis because, he argued, the capacity to imitate (as well as several other higher mental faculties) was not unique to the most highly evolved form, adult Western man, but could be found elsewhere in the phylogenetic scale. In fact, Romanes claimed, imitation reaches its highest level of perfection in slightly inferior forms: monkeys, children, savages, and idiots. So, if one could find evidence of learning by observation or imitation in nonprimate animals, one would be providing strong evidence of a continuity of mental faculties and hence providing support for the Darwinian notion of the evolution of human mind by natural processes.

George Romanes was a strong proponent of the view that learning by observation is central to behavior acquisition in animals. In 1882, Romanes published an influential monograph, *Animal Intelligence,* in which he provided more than five hundred pages of anecdotal description and interpretation of instances in which animals exhibited rather remarkable intellectual powers in the solution of problems they encountered in their natural environments. However, many of the examples of animal learning in nature reported by Romanes and his correspondents were fanciful at best. For example, mice in Iceland were said to have been observed storing supplies of berries in dried mushrooms, loading these rations onto dried cow-droppings, and then launching their improvised, provisioned vessels and guiding them across rivers using their tails as rudders. It was assumed that the mice had originally acquired these abilities by observing and imitating humans, and that the capacities to store provisions and construct and steer rafts had become traditional in some mouse populations. However, not all of the evidence of intelligence in animals described by Romanes was quite so unlikely, and some was central to future developments in the study of the learning capacity of animals.

Possibly the most historically important of Romanes's many cases of supposed "imitation learning" concerned a cat that belonged to his coachman. This animal had learned, without formal tuition of any kind, to open a latched door in Romanes's yard by jumping up and grabbing the latchguard with one forepaw, depressing the thumbpiece with the other forepaw, and simultaneously pushing at the doorpost with her hind legs. Romanes argued that the cat, in the absence of any other source of information, must have observed that humans opened the door by grasping the handle and moving the latch. Then, said Romanes, the cat must have reasoned, and I quote, "If a hand can do it, why not a paw?" Finally, strongly motivated by this insight, the cat attempted to and succeeded in opening the door.

The problem with Romanes's interpretation, of course, is that simple observation of an animal behaving in an uncontrolled environment provides little useful information about the processes responsible for the development of the animal's behavior. It is impossible to tell from simply watching an animal perform an act in an uncontrolled setting what the necessary antecedent conditions of that performance are.

Experimental animal psychology in North America may well have arisen out of Edward Thorndike's irritation with the excesses in Romanes's *Animal Intelligence:* its anecdotal method, its speculative conclusions, and most particularly its insistence on the importance of observational learning and tradition in the development of the behavior of animals. In the late 1890s Thorndike brought the door-opening behavior of cats, described by Romanes, into the laboratory and studied the acquisition of solutions to a variety of mechanical problems in controlled and replicable situations. In one of Thorndike's experiments, food-deprived cats were individually placed in a wooden cage and observed as they learned to depress a treadle located in the center of the floor of the apparatus in order to escape confinement and gain access to a food bowl placed outside the cage (figure 1). As is well known, on the basis of the results of his

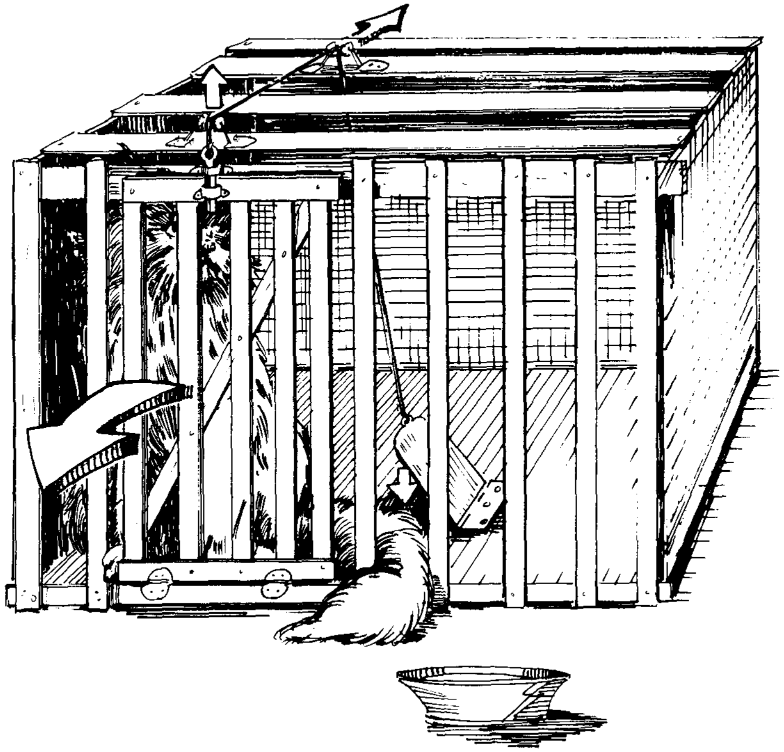

Figure 1 One of Edward Thorndike's puzzle boxes, designed for the study of trial-and-error learning in cats. When the cat steps on the treadle in the center of the floor, the door opens and the cat can escape confinement and gain access to food. (Illustration by Richard Swartz, based on a drawing supplied by B. G. Galef, Jr.)

studies in a variety of such puzzle boxes, Thorndike (1911) proposed that animals learn to solve *all* such problems, including presumably the opening of garden gates, as the result of their *individual interactions* with the environment, by a gradual process of trial-and-error learning. Less generally appreciated is Thorndike's explicit rejection, on both theoretical and empirical grounds, of the possibility of learning by observation. Thorndike had found that animals in general, and cats in particular, did not learn to get out of puzzle boxes either by observing other cats do so or by observing humans demonstrate solutions. In fact, Thorndike found that observation of a trained demonstrator by a naive individual sometimes interfered with the gradual process of trial-and-error learning by which naive individuals acquire solutions to a variety of problems.

Of course, it cannot be inferred from the lack of evidence for true imitation learning that other sorts of social learning might not be important to animals in their natural environments. (Thorndike himself was careful to point out that what he called "semi-imitative" phenomena, the "indirect results of instinctive acts" of various kinds, could accelerate learning.) In fact, there are certain behavioral phenomena in nature that appear to *require* explanation in terms of social learning of some kind—behavior patterns that are usually referred to as "traditional" (Galef 1976). If you compare the behavior of members of a single species living in nature in different social groups, as any number of field biologists have done, you will often find that many of the members of one social group will exhibit a pattern of behavior totally absent in other groups. Such intergroup differences in behavior are most commonly observed in patterns of food selection or in the motor patterns involved in food acquisition.

Field biologists, observing such intergroup variation in behavior, have long assumed that such animal traditions are transmitted from individual to individual within a group by observational learning or imitation. However, data from many psychology laboratories over many years suggest that observational learning and imitation are not very important processes in behavior acquisition, at least not in nonprimates. So there remain important questions as to the processes supporting the development and maintenance of the "traditional" patterns of behavior to be observed in many nonprimate vertebrate social groups.

Experimental Analysis of the Learning of a Tradition in Wild Rats

For the past decade my students and I have been studying the role of social process in the development of traditional patterns of behavior in wild Norway rats. In the next few pages I will describe one of several instances in which we have attempted to determine the causes of idiosyncratic feeding patterns exhibited by our animals. We began with field observation of a traditional pattern of behavior, brought the phenomenon into the laboratory, and then attempted to analyze the social learning mechanisms supporting that behavior (Galef 1982; Galef and Clark 1971).

Some years ago an applied ecologist, Fritz Steiniger, was working for the German government as a rodent control officer. He noticed a rather peculiar thing. Steiniger found that if he employed some poison bait in an area for an extended period of time, he would have considerable initial success, with the rats eating lots of posion and dying in large numbers. Later, however, acceptance of the bait was very poor. Steiniger noted in particular that young rats born to adults that had survived poisoning rejected the poisoned bait without ever even sampling it themselves. These young fed exclusively on safe diets available in their colony territory and totally avoided contact with the poison bait their elders had previously learned to avoid.

This is a robust phenomenon and relatively easy to capture in the laboratory. In our basic experiment, we established colonies consisting of two male and four female adult wild rats in 3-by-6-foot enclosures each containing four wooden nest-boxes. Water was continuously available and food was presented to the colony for 3 hours a day in two food bowls located about 2½ feet apart. Each bowl contained one of two nutritionally adequate diets, each discriminable from the other in color, texture, taste, and smell. For simplicity, I will refer to these two diets as diets A and B in all that follows.

The adult members of our colonies were trained to eat one of the diets presented each day and to avoid the other because it was laced with lithium chloride, an illness-inducing agent.

Under these conditions our wild rats rapidly learned to avoid eating the contaminated diet and, most important, continued to avoid the previously contaminated diet for some additional weeks when they were offered uncontaminated samples of it. So we have colonies of adult wild rats eating either diet A or diet B, and avoiding the alternative because of its previous association with illness.

The experiments proper began when litters of pups that were born to colony members left their nest-site to feed on solid food for the first time. We observed the adults and pups throughout daily 3-hour feeding periods on closed circuit television and recorded the number of times the pups ate from each of the two food bowls, now containing uncontaminated samples of diet A and diet B. We found that pups born to a colony trained to avoid eating diet B ate only diet A, the diet that their parents had been trained to eat. Pups born to a colony trained to avoid diet A ate only diet B and never even made contact with diet A (figure 2). Observations of more than 240 wild rat pups during their first two weeks of feeding on solid food have revealed only a single individual that ate any of the diet that the adults of its colony had learned to avoid.

After a litter of pups had been feeding on solid food for two weeks, we transferred them to a new enclosure, similar in size but different in layout from their original home. Here, without the adults of their colony, the pups were again offered a choice between uncontaminated samples of diets A and B. The amount of each diet eaten by the pups in this situation was determined by weighing food bowls before and after each feeding session. We found that the pups continued for 8 to 10 days to prefer the diet that the adults of their colony had eaten, even though the pups were now living and feeding without contact with those adults.

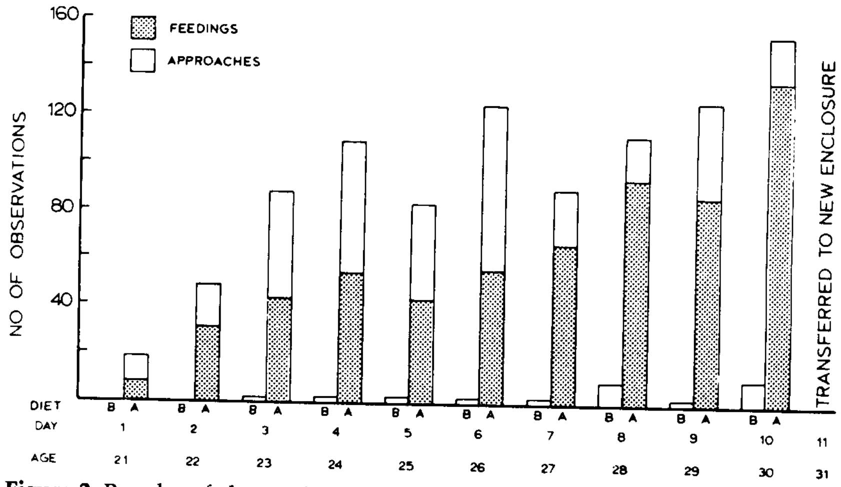

Figure 2 Results of the study demonstrating the role of social influence on diet selection in weanling wild rats. Although food B is normally preferred by rats, the adults learned to avoid it when it was experimentally altered to make them ill. The graph shows that weanling rats, who never experienced illness associated with food B, also showed the adult pattern of rarely approaching and never eating food B.

Taken together, these observations demonstrate, as Steiniger suggested, that adult rats can, in some fashion, lead their offspring to feed solely on a safe diet in an environment containing food known by the adults to have been poisoned. The data also show that the food preferences learned in the presence of adults continue to affect the diet preference of pups for some time after their removal from direct adult influence. So there can exist traditions in the food preferences of colonies of wild rats. The important question is how are such traditions established and maintained in a wild rat population?

Over the last few years, my students and I have found a number of ways in which adult wild rats can induce their young to wean to a given food. For example, we have found that the physical presence of adults at a feeding site attracts pups to that feeding site and markedly increases the probability of young rats weaning to the food located there. If one establishes a colony of adult wild rats in a large enclosure (12 by 8 feet) makes diet A continuously available in two food bowls located 10 feet from the nesting area, and continuously (24 hours a day) monitors behavior at the food bowls, one can determine the conditions under which each individual pup in a litter eats it first meal of solid food (figure 3). We have observed nine individually marked pups from three litters take the first meal of solid food and all nine ate their first meal under exactly the same circumstances. Each ate its first meal while an adult was eating and each ate at the same food bowl as the feeding adult, not at the other food bowl 1.5 feet away. Given the observed temporal and spatial distributions of adult meals, the probability of those conditions occurring nine times in succession by chance was very small indeed, less than four in a thousand. So the presence of an adult at a feeding site serves to attract pups to that site and to cause pups to initiate feeding there.

In addition to being able to influence a pup's choice of feeding site, and thus indirectly its food preference, the mother of a litter of pups can also directly influence her own pups' dietary preference. We have conducted an experiment much like the first one described above, but with one important difference. Colonies of adult rats were again housed in 3-by-6-foot enclosures, but adults were removed to a

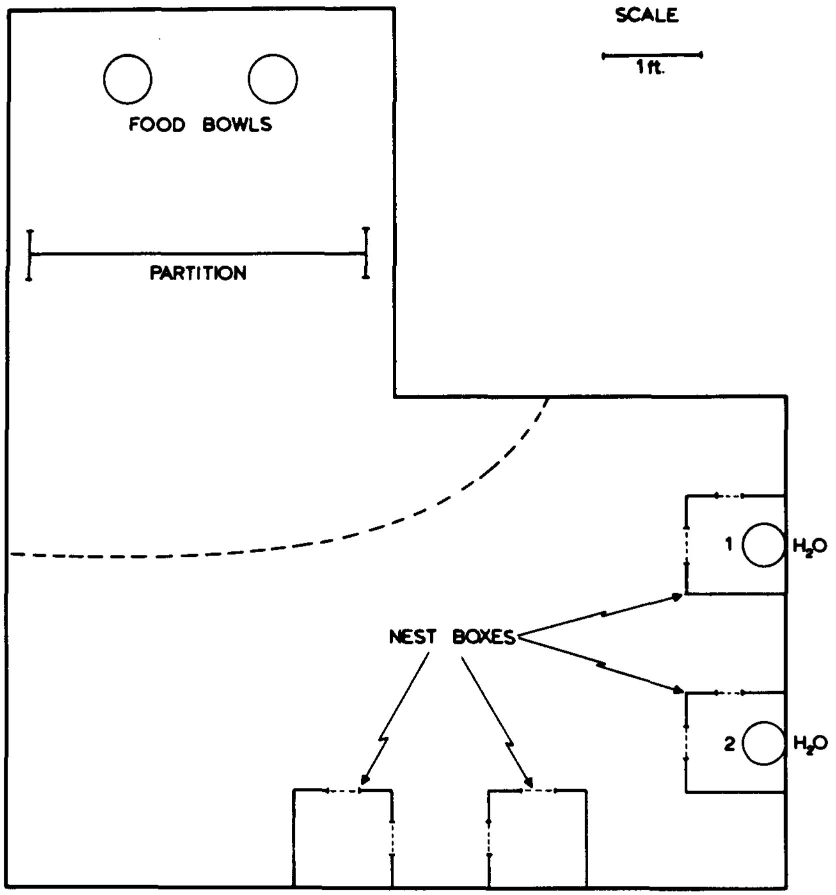

Figure 3 Floor plan of the enclosure used for observing the first meals eaten by wild rat pups. The area above the dashed line is continuously monitored on closed circuit television. Adults established nests for their young at 1 and 2.

separate cage for 3 hours each day, where they were fed either diet A or diet B, depending on the experimental condition to which their colony was assigned. While the adults were out of the colony enclosure, the pups were presented with two standard food bowls, one containing diet A and the other diet B. We found that the diet eaten by the adults profoundly affected the food choice of the pups even though the adults and young had no opportunity to interact directly in a feeding situation. Once again pups from colonies of adults trained to eat diet B ate diet B, while those from colonies of adults trained to eat diet A preferred that diet.

Our research indicates that the milk of a lactating female rat contains cues directly reflecting the flavor of her diet. We believe that at weaning, as the result of prior exposure to these flavor cues, rat pups exhibit a preference for a diet of the same flavor as the diet that their mother had been eating during lactation (Galef and Sherry 1973).

Fritz Steiniger was right. The learned feeding preferences of adult wild rats can be socially transmitted to their young, reducing the probability that the young will ingest toxic food.

Edward Thorndike was also right. The indirect results of what might be conceived of as instinctive acts, in this case the tendency of rat pups to approach adults and to suckle from their mother, can result in introduction of the young to their parents' diet and consequent *apparent* imitation of learned adult food preferences by the young. So here we have a case in which an animal tradition rests not on imitation or observational learning, but instead on some rather simple sorts of exposure learning.

Social influences on foraging behavior and diet selection are important to rats and are supported by a range of simple but elegant social learning processes. One of these that we are analyzing now is quite powerful. Anyone seeing rats in the wild exhibiting the behavior I am about to describe might be convinced that they are very clever indeed. The explanation, however, is really quite simple.

The laboratory procedure we used was designed to mimic a situation in which a foraging rat ingests a food item at some distance from its burrow, returns to the burrow, and then interacts with a familiar burrow-mate that subsequently selects a food item to eat. We were interested to know whether, as the result of such interaction at a distance from a feeding site, a burrow resident could acquire information concerning the food a returning forager had eaten (Galef and Wigmore 1983).

In brief, our procedure involved feeding one rat (a demonstrator) one of two novel-tasting diets, either cocoa-flavored diet or cinnamon-flavored diet, and then allowing the demonstrator to interact with a second rat (an observer) for 15 minutes. Immediately following this brief period of interaction between demonstrator and observer, the demonstrator was removed from the experiment. Then, for 60 hours, the observer was offered a choice between two food cups, one containing cinnamon-flavored diet and the other containing cocoa-flavored diet. We weighed the food cups every 12 hours and found, much to our surprise, that observers whose demonstrators had eaten cocoa-flavored diet ate much more cocoa-flavored than cinnamon-flavored diet, while observers whose demonstrator had eaten cinnamon-flavored diet ate much more cinnamon- than cocoa-flavored diet. The effects of the demonstrators' diet on the observers' diet preference were still very strong 60 hours following interaction of observer and demonstrator.

Rats can communicate to one another information concerning diets ingested at a time and place distant from the locus of communication. Further, information passing from demonstrator to observer concerning the food the demonstrator has eaten has profound effects on the subsequent food preferences of observers. How do the rats influence one another's food preferences in this way? Quite simply, when an observer rat is exposed to the smell of a food item on the breath of a demonstrator rat the observer subsequently exhibits a strong preference for the food eaten by the demonstrator.

My students and I have developed several converging lines of evidence each of which is consistent with the hypothesis that olfactory cues passing from demonstrator to observer cause observers to prefer their demonstrator's diet. I will describe two of these lines of evidence very briefly.

If, after the demonstrator has eaten either cocoa- or cinnamon-flavored diet, and before it interacts with an observer, the demonstrator is anesthetized, taped to a stand, and placed for 15 minutes with its nose 2 inches from a screen that separates the sleeping demonstrator from its observer, the message still gets through; the observer interacting with a sleeping demonstrator 2 inches away still exhibits during testing a strong preference for that demonstrator's diet (figure 4). Which tells us two things: first, the effective message is emitted in a passive way by the demonstrator and is not elicited by the observer; and second, no physical contact between demonstrator and observer is required for information transfer to occur. The important cue can be transmitted over some distance; therefore, it is not a taste cue, which strongly suggests that olfactory cues (smells) are carrying the message.

In another experiment, we found that if we render an observer anosmic (unable to smell) by rinsing its nasal cavity with zinc sulfate solution prior to the time that an observer interacts with its demonstrator, the observer subsequently fails to exhibit a preference for its demonstrator's diet during testing. Control observer rats, whose nasal passages have been rinsed with a neutral saline solution prior to their interaction with demonstrators, do show a strong tendency to eat the same diet that their demonstrator has eaten. Thus, olfactory sensitivity in observers is necessary for information transfer to occur.

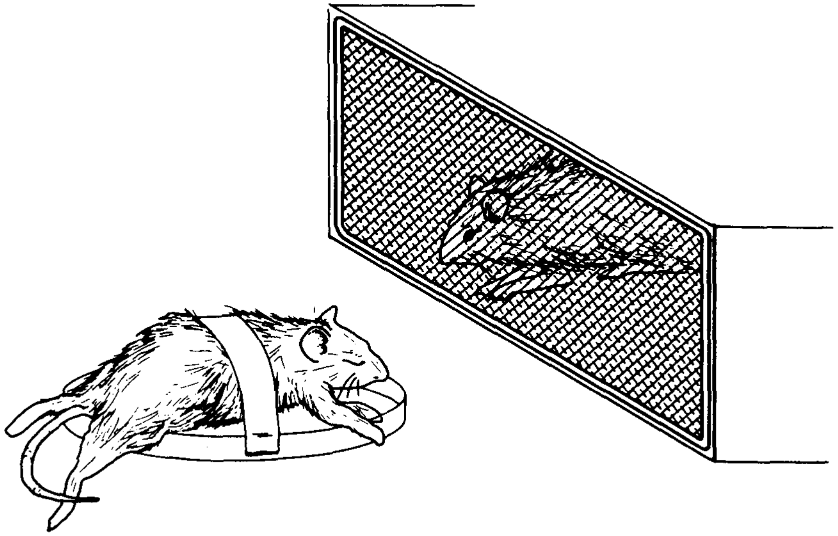

Figure 4 An awake "observer" rat with no established preference for either of the strong-smelling experimental foods is exposed to the sight and odor of an anesthetized "demonstrator" rat who has eaten one of the foods. The observer will later show a strong preference for the food eaten by the demonstrator, indicating that food preferences can be transmitted passively and without physical contact.

Once again we have *apparent* imitation of one rat by another resting on a very simple social learning process. Smelling a food on the breath of a conspecific induces a preference for that food and apparent imitation of demonstrators by observers.

Conclusions

Several well-known examples of animal traditions described in the literature have not yet been analyzed in detail. I am sure that many people have heard of the monkeys of Koshima Islet in Japan that clean sand from the skin of sweet potatoes by dipping the potatoes in water before eating them, or have read about the troop of monkeys whose members have learned to sort wheat from sand by throwing handfuls of the mixture onto water. Then there are Jane Goodall's chimpanzees in the Gombe reserve that fish for termites using twigs as tools, and several species of British birds that, as I mentioned earlier, have learned to open milk bottles and eat cream from the surface of the milk. While there is no doubt about the reality of such behavioral phenomena, it is premature to assume that such patterns of behavior pass from one individual to another as the result of imitation or observational learning. There is no reason to believe that such traditional behaviors are evidence of any particularly great intellectual prowess in those animals that exhibit them. The fact of the existence of a traditional behavior pattern does not tell us anything about how the traditional behavior was acquired or transmitted.

It is important to keep in mind that simple acquisition processes can be responsible for rather complex behavioral outcomes. Until the processes of acquisition of such traditions can be examined in detail under controlled conditions, they remain thought-provoking observations, not evidence of the reality of special mental abilities in those creatures that exhibit traditions. A healthy skepticism and a commitment to empiricism are necessary for the development of understanding of the social learning processes resulting in traditions in animals.

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