THE BEHAVIOR OF THE LABORATORY RAT

A Handbook with Tests

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Systematic observation of free-living mammals and birds often reveals differences in the behavior of species members that live in different areas. Such geographic variation in the behavior of chimpanzees and orangutans is particularly well documented (Whiten et al., 1999; van Schaik et al., 2003) and is widely known because of the attention it has received in the popular press. However, before the recent dramatic increase in field studies of the great apes, it was not unreasonable to propose, as did Steiniger (1950, p. 369), that "the [Norway] rat appears especially able to develop local traditions, more so perhaps than other more-closely examined mammals, possibly including the anthropoids."

NORWAY RATS

Norway rats are arguably the most successful, and surely the most widely distributed, non-human mammals on Earth. Breeding populations have been reported from Nome, Alaska, at 60 degrees North latitude, where rats feed on human garbage, to South Georgia Island, at 55 degrees South latitude, where tussock grass, beetles, and ground-nesting birds provide sustenance for colonies of Norway rats.

As the preceding two examples suggest, much of the success that rats enjoy results from the extraordinary range of foods that they are able to exploit, and as in the great apes, much of the known variation in behavior in free-living Norway rats involves foraging behavior. Rats in West Virginia catch and

eat fingerling fish in trout hatcheries, whereas those living on Norderoog island in the North Sea stalk and kill ducks and sparrows. Yet other R. norvegicus living along the banks of the Po River in Italy dive for and feed on mollusks living on the bottom of the river, while their fellow rats in Japan scavenge dead fish that wash up on the seashore. Such naturally occurring variability in feeding behavior has been the focus of most experimental studies of social learning in the species.

PREVIEW

I begin the present brief review of the literature on social influences on food choices of Norway rats with a description of fieldwork strongly suggesting that interactions between adult free-living rats and their young can determine which foods the young come to eat. I then describe very briefly several behavioral processes that have been shown in the laboratory to be sufficient to influence food choice in young rats. Last, I describe in somewhat greater detail a type of social influence on rats' food preferences that has already proved to be useful in studies of the physical substrates of learning and memory.

FIELD OBSERVATIONS
OF NORWAY RATS

Fritz Steiniger, an applied ecologist whose professional interest lay in enhancing the effi-

ciency with which rodent pests could be exterminated, was the first to report difficulties in controlling pest populations of Norway rats using the economically desirable method of placing permanent stations containing poisoned bait in rat-infested areas (Steiniger, 1950). Steiniger found that although rats ate ample amounts of poison bait and died in large numbers when a permanent bait station was first introduced into their colony's territory, later acceptance of the bait by colony members was very poor, and colonies targeted for extermination soon returned to their initial sizes.

Steiniger reported that permanent bait stations failed because young rats, born to colony members that had survived their initial contact with the poisoned bait and had learned to avoid eating it, refused to even taste the bait that the adults of their colony were avoiding.

A LABORATORY ANALOGUE

Avoidance by young wild rats of a food that adults of their colony have learned to avoid eating is a robust phenomenon that is easily observed in rats transferred from their natural habitats to laboratory enclosures. We captured adult wild rats (R. norvegicus) on garbage dumps in southern Ontario, transferred them to our laboratory, and placed them in groups of five or six in 2 m² enclosures that each contained nesting boxes and nesting materials and provided ad libitum access to water. For 3 hours each day, we offered each colony two foods that differed in taste, smell, texture, and color (Galef and Clark, 1971b).

To begin a typical experiment, we introduced a sublethal concentration of toxin into one of the two foods that we gave our captives to eat daily. The rats soon learned to avoid eating the poisoned food, and for weeks thereafter, they avoided eating the food that had been noxious, even when we gave them uncontaminated samples of it (Garcia et al., 1966).

After we had trained our colonies to avoid one of the two foods that we placed in their enclosure each day, we waited for female colony members to give birth and for their young to grow to weaning age. As the young approached independence, we started to observe their colony on closed-circuit television throughout daily feeding periods. When the young started to eat solid food, we recorded the frequency with which they ate each of the two foods in their cage: one that adult colony members were eating and the other that the adults had learned to avoid.

We found, without exception, that weaning rats ate only the food that the adults of their colony were eating and totally avoided the alternative food that the adults had learned to avoid. Even after we removed pups from their natal enclosures, housed them individually, and offered them the same two foods that had been available when they were in their colony cages, pups continued to eat only the food that the adults of their colony had eaten (Galef and Clark, 1971b) (Fig. 34-1).

ANALYSIS OF THE PHENOMENON

My students and I have spent much of the past 30 years determining how the food choices of adult rats might influence those of the young they rear (see reviews in Galef, 1977, 1988, 1996a, 1996b). Over those years, those working in my laboratory and in other laboratories as well have discovered many different ways in which the food choices of young rats are affected by social interactions with conspecific adults.

Prenatal Effects
Fetal rats exposed to a flavor while still in their mother's womb (through injection of a flavored solution into the dam's amniotic fluid) will, when grown, drink more of a solution containing that flavor than will control rats that lack prenatal exposure to it (Smotherman, 1982). Even feeding a food with a strong odor to a female rat while she gestates a litter
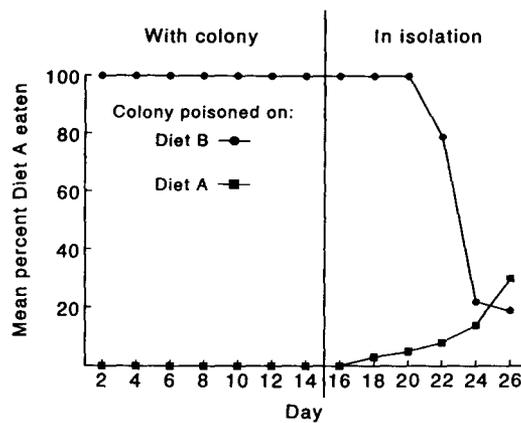
Figure 34–1. Rat pups born into colonies trained to avoid eating either diet A or diet B are offered a choice for 3 hours per day between diet A and diet B. Abscissa shows the days since pups started to eat solid food; ordinate, relative frequency with which pups from the two types of colony ate diet A. Pup diet choice while still in their natal colonies (*left*) and the amount of diet A eaten, as a percentage of total amount eaten, by pups after transfer to individual cages and offer of diet A and diet B for 9 hours per day (*right*). (Data from Galef and Clark [1971].)

suffices to enhance her postnatal preferences of her young for the odor of that food (Hepper, 1988).

Effects during Suckling

Flavors of foods that a rat dam eats while lactating affect the flavor of her milk, and exposure to milk flavored by the foods that a lactating dam eats while rearing her young affects the food preferences of her pups at weaning (e.g., Galef and Sherry, 1973).

Effects during Weaning

Galef and Clark (1971a) used time-lapse video recordings to observe each of nine wild rat pups that had ad libitum access to solid food take its first meal. All nine pups ate solid food for the first time under the same circumstances. Each ate at the same time that an adult member of its colony was feeding, which was highly unlikely given the temporal distribution of adult meals, and each ate at the same place an adult was feeding, not at an alternative feeding site a short distance away.

Even an anesthetized adult rat placed near one of two otherwise identical feeding sites made that site far more attractive to pups than one without an adult present (Galef, 1981).

By comparing the circumstances in which intact and visually deprived rats weaned, we found that intact pups use visual cues to approach adults from a distance when selecting a place to eat solid food for the first time.

Effects of Snatching Food from Adults

Young rats, like the young of many other mammalian species, seem to be especially interested in the particular piece of food that someone else is eating. Juvenile rats will walk across a cage floor carpeted with food pellets and steal an identical pellet from the mouth or paws of an adult or a peer that is eating it. Young rats that have stolen a pellet of unfamiliar food from the mouth of a conspecific subsequently show a greater preference for that food than do young rats that have eaten an identical food pellet taken from the floor of their cage (Galef et al., 2001).

Effects of Scent Marks and Scent Trails

While feeding, adult rats deposit olfactory cues both on and around a food they are eating (Galef and Beck, 1985). Such residual odors attract pups and, like the physical presence of an adult rat at a feeding site, cause young rats to prefer marked sites. Further, when an adult has finished eating and travels back to its burrow, it deposits a scent trail that directs young rats seeking food to the location at which the adult ate (Galef and Buckley, 1996).

IMPLICATIONS OF REDUNDANCY

Redundancy in the behavioral processes that support social influences on food choice in rats is in itself important. Such redundancy suggests that for rats, as for the honeybees studied by Karl von Frisch (1967), socially acquired information substantially increases for-

aging efficiency. Indeed, it is easy to demonstrate that, for naïve rats residing in an environment where foods containing needed nutrients are difficult to identify, the presence of conspecifics that have already learned to select an appropriate diet can make the difference between life and death. Young rats that would have died because of an inability to learn independently to focus their intake on the sole protein-rich food available among a cafeteria of foods available to them learned rapidly to eat that food when caged with adult conspecifics trained to do so (Beck and Galef, 1989).

IS THERE ANYTHING SPECIAL ABOUT SOCIAL LEARNING?

Our analyses have indicated that in most instances of social influence on the food choices of young rats, interaction between adult and young rats has resulted in introduction of the young to one food rather than another. Adults bias young either to initiate feeding on foods that the adults are eating, rather than on alternative foods, or to start to feed at feeding sites that the adults are visiting, rather than at alternative sites. Differences in the responses of young rats to familiar and unfamiliar foods and locations are then responsible for much of the influence of adults on the choices of juveniles with which they interact (Galef, 1971b).

Such effects of socially induced familiarity on food choice are particularly pronounced in genetically wild Norway rats that are extremely hesitant to eat unfamiliar foods (Barnett, 1958). The extreme neophobia of wild rats makes introduction of juveniles to one food rather than another a critical event in the development of their feeding repertoires (Galef and Clark, 1971b).

However, not all of the social influences on the food choices of rats reflect a simple social biasing of naïve young rats to eat one food rather than another together with neophobia. In the case discussed in the next section, so-

cially induced food preference seems to result from a behavioral process that directly alters the affective response of young rats to foods experienced in a social context (Galef et al., 1997).

FLAVOR CUES ON THE BREATH OF RATS

In the early 1980s, scientists in several laboratories demonstrated that after a naïve "observer" rat interacts with a recently fed conspecific "demonstrator," the observer exhibits a substantial enhancement of its preference for whatever food its demonstrator ate (Galef and Wigmore, 1983; Strupp and Levitsky, 1984). For example, after naïve observer rats interacted briefly with conspecific demonstrators fed either a cinnamon- or a cocoa-flavored diet, the former group of observers preferred cinnamon-flavored food, whereas the latter preferred cocoa-flavored food, if offered a choice between the two (Fig. 34–2).
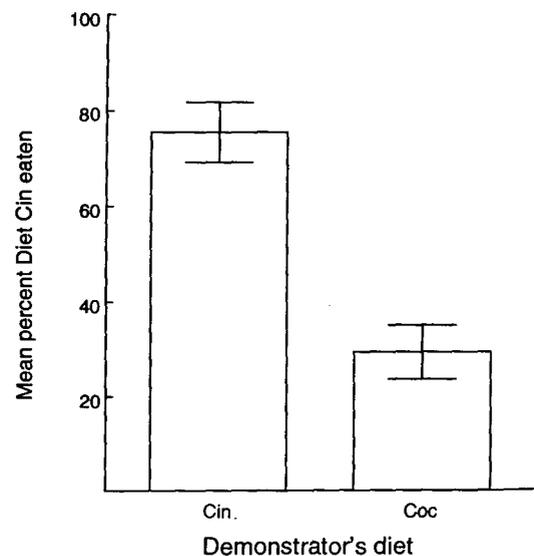

Figure 34–2. Amount of cinnamon-flavored diet (Diet Cin) eaten, as a percentage of total intake over 22 hours, by observer rats that interacted with demonstrators fed either Diet Cin or cocoa-flavored diet (Diet Coc). Error bars show 1 SEM. (Data from experiments like those described in Galef and Wigmore [1983].)

The effects of a single brief exposure to recently fed demonstrator rats on the food choices of their observers are both surprisingly powerful and surprisingly long lasting. Many observer rats taught to totally avoid ingesting a food by following its ingestion with an injection of toxin, and then placed with demonstrator rats that have eaten the food that their observers had learned to avoid, totally abandoned their aversions. Similarly, most observer rats that interacted with a demonstrator fed a diet adulterated with cayenne pepper (an inherently unpalatable taste to rats) subsequently preferred peppered to unadulterated diet (Galef, 1986b). Such effects of demonstrator rats on the food choices of their observers can be seen a month or more after a demonstrator and observer interact (Galef and Whiskin, 2003).

ANALYSIS

The behavioral process that produces such social influence on the food choices of observer rats is now quite well understood. Olfactory cues passing to observer rats from demonstrators cause observers to increase their preferences for the foods that their respective demonstrators ate (Galef and Wigmore, 1983). Observers sniff at the mouths of demonstrators, and this sampling of a demonstrator's breath is both necessary and sufficient for demonstrators to influence the later food choices of observers (Galef and Stein, 1985).

Both food-related odors escaping from the digestive tract of a demonstrator and the scent of bits of food clinging to a demonstrator's fur and vibrissae allow observers to identify the food that a demonstrator has recently eaten. And after an observer rat experiences simultaneously the scent of a food and rat breath, the observer shows an enhanced preference for the food the scent of which it experienced together with rat breath (Galef and Stein, 1985).

Gas chromatography performed on samples of rat breath has shown that it contains two sulfur compounds: carbon disulfide and carbonyl sulfide. Rats exposed to a food dusted onto either the head of an anesthetized conspecific or a piece of cloth moistened with a dilute solution of carbon disulfide subsequently show an enhanced preference for that food. To the contrary, rats exposed to a food, that had been dusted onto the head of a dead conspecific, onto the rear of a live conspecific or onto a piece of cloth moistened with distilled water do not develop a similar preference (Galef et al., 1988) (Fig. 34-3). Thus, experience of carbon disulfide, a natural constituent of rat breath, in conjunction with a food odor, like experience of rat breath in conjunction with a food odor, is sufficient to enhance preference for the food.

SYNTHESIS

The breath of humans, like the breath of rats, contains trace quantities of carbon disulfide. As would be expected on the hypothesis that experience of food odors together with car-
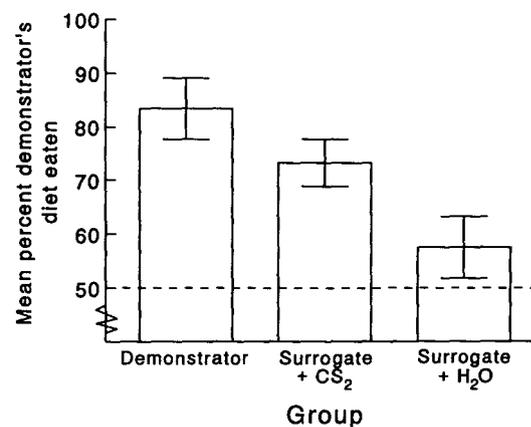

Figure 34-3. Observer rats interacted with either an anesthetized demonstrator rat or a cloth "surrogate" demonstrator. The demonstrator with which each observer interacted had been powdered with either cinnamon- or cocoa-flavored diet. Surrogates were moistened with either a dilute aqueous solution of CS_2 or an equal amount of distilled water. The figure indicates the mean percent of each observer's total intake that was the diet with which its demonstrator or surrogate had been powdered. Error bars show 1 SEM. (Data from Galef et al. [1988].)

bon disulfide induces food preferences in rats, when a human "demonstrator" eats a flavored food and breathes on a rat, the rat's preference for the food that its human demonstrator ate is markedly enhanced (Galef, 2001).

LIMITATIONS

Surprisingly, rats do not learn to avoid a food by interacting with a sick or an unconscious demonstrator that has eaten it. To the contrary, rats show an increased preference for a food that was eaten by an ill conspecific with which they interacted (Galef et al., 1990).

Further, exposure to an odor in conjunction with a conspecific does not enhance the general affinity of a rat for that odor; exposure to an odor in a social context that profoundly affects food preference has no effect on the odor preferences of rats in other contexts. For example, rats that have interacted with a conspecific that has eaten a cinnamon-flavored diet prefer cinnamon-flavored food but show no enhancement of their preference for cinnamon-scented nest materials or cinnamon-scented nest sites (Galef and Iliffe, 1994). Such findings suggest that social induction of food preference is a learning process evolved specifically to facilitate foraging rather than other activities of rats.

EXTENTIONS

Rats can use information concerning foods that other rats have eaten in some interesting ways. For example, after "observer" rats had an opportunity to learn where in a three-arm maze each of three distinctively flavored foods were to be found, we let each observer rat interact briefly with a demonstrator rat that had eaten one of those three foods. Without any specific training, the observers went directly to the arm of the maze where they had learned that the food that their demonstrator had eaten was usually located (Galef and Wigmore, 1983). Obviously, rats can integrate their cognitive map of food distribution with socially acquired information about the current availability of foods to increase the efficiency with which they forage.

APPLICATION TO STUDIES OF NERVOUS SYSTEM FUNCTION

Socially induced enhanced diet preference provides an efficient and reliable way to induce a learned appetitive behavior in rats (or mice, gerbils, hamsters, voles or bats) that, like other types of learned behavior, can serve as a dependent variable in studies of brain function. Neuroscientists have used the socially induced change in food preference described here to study the effects of manipulations of the neural substrate on learning and memory (Burton et al., 2000; Winocur et al., 2001; see Galef, 2002, for further references). As one might expect, both direct and genetic manipulations of the nervous system affect social learning of food preferences.

There are several advantages in using socially learned food preference as a dependent measure in studies of brain function: (1) learning occurs in a single trial, (2) little or no skill is needed to train subjects, (3) no special equipment is needed to train subjects, and (4) subjects need never be deprived or stressed. The procedure for inducing social enhancement of food preference consists of three straightforward steps. First, a demonstrator rat is placed on a feeding schedule and given one of two distinctively flavored foods to eat. Second, each demonstrator is placed together with an observer, and demonstrator and observer rats are allowed to interact for 15 minutes or longer. During this period of interaction, observers have the opportunity to smell the scented food on the breath of their respective demonstrators. Last, each observer is given a choice between the two distinctively flavored foods that were offered to demonstrators in the first step (Galef, 2002) (Fig. 34-4). In the third step, observers invariably show an enhanced preference for whichever
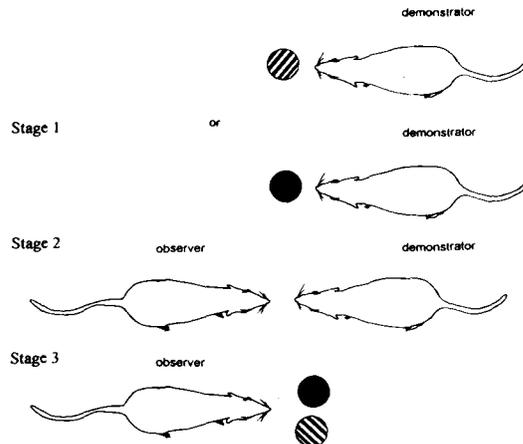
Figure 34–4. Schematic of the three stages of an experiment demonstrating social influence on the diet preferences of observer rats'. In stage 1, each demonstrator rat ate one of two distinctively flavored foods. (From Galef [2002]. Reprinted with permission of John Wiley & Sons, Inc.)

flavored food was eaten by their respective demonstrators.

The effect is robust. Demonstrator and observer can be male or female, young or old, previously familiar or unfamiliar with one another, and genetically related or unrelated to one another (Galef et al., 1984). Demonstrators can ingest almost any scented liquid or solid before interacting with their observers. There can be a delay of several hours between when a demonstrator is fed and when it interacts with its observer. Demonstrators can be separated from their observers by a hardware-cloth screen while they interact, and interaction can take place in the home cage of demonstrator or observer or in a neutral arena. There can be a delay of weeks between when demonstrator and observer interact and when the observer is tested. Invariably, if demonstrators that have recently ingested a distinctively flavored substance are placed for a few minutes together with observers that are otherwise unfamiliar with the flavor of the food that was eaten by their respective demonstrators, the observers subsequently show significant enhancement of their relative intake of that food.

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