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Norway Rats' Communication About Foods and Feeding Sites

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ABSTRACT

After interacting with a recently fed "demonstrator" rat (*Rattus norvegicus*), a naïve "observer" rat exhibits substantial enhancement of its preference for whatever food its demonstrator ate. Such social effects on food preference in rats are surprisingly robust and able to reverse both congenital flavor preferences and poison-induced, learned flavor aversions. Analysis of the pheromonal signals emitted by demonstrator rats that alter the food preferences of their observers indicates that experience of CS₂ (a substance present in rat breath) together with the odor of a food is sufficient to enhance an observer rat's subsequent preference for the food. Adding CS₂ to a food substantially increases intake of that food by both rats and mice (*Mus domesticus*), suggesting that CS₂ could be used to enhance intake of poison baits by rodent pests. Recent analyses of the use by rats of odor trails indicate that additional pheromones attractive to rats remain to be described.

KEY WORDS

food selection, poison avoidance, pheromones, communication, Norway rats, urine, trails

INTRODUCTION

For more than 25 years, my students, coworkers, and I have been studying the many ways in which Norway rats (*Rattus norvegicus*) are able to influence one-another's selections of foods to eat (for reviews, see Galef 1977, 1988, 1990, 1996). The existence of communicative systems, allowing one rat to influence the food choices of others of its species, provides an opportunity for those interested in control of rodent pests. If the signals that rats (or other rodents) use to communicate among themselves about which foods are safe to eat can be identified and synthesized, it may be possible to use the species-typical communications of rodents to lead them to eat poison baits, to enter traps, or to engage in other behaviors that are not really in their own best interest.

Below, I first describe the results of an analysis that has been underway in my laboratory for more than 10 years of a complex of intraspecific olfactory signals used by Norway rats in deciding what foods to eat. I then present evidence consistent with the view that a rodent attractant

developed as a result of that analysis can increase rats' ingestion of baits. Finally, I describe the first stages of an analysis of a second rodent olfactory communication system that may lead to discovery of pheromones that affect the paths chosen by rats.

SOCIAL INDUCTION OF FOOD PREFERENCES IN NORWAY RATS

Exploring the Phenomenon

The procedure that we used in our studies of social influence on the food preferences of Norway rats was designed to mimic a natural situation in which a foraging rat eats a food at some distance from its burrow, returns to its burrow, and then interacts with a burrow-mate that subsequently selects a food to eat (Galef and Wigmore 1983). We wanted to know whether the burrow mate, while interacting with a successful forager at a distance from a feeding site, could extract information from the forager about foods it had eaten and whether the burrow mate would use that information when, sometime later, it selected a food to eat.

During our experiments, subjects were housed and tested in demonstrator-observer pairs in large wire-mesh cages that were divided into two equal parts by a screen partition. Treatment of each pair of subjects during the experiment was as follows (see Figure 1):

- Step 1: Demonstrator and observer were first maintained together with ad libitum access to pellets of rat chow for 2 days to become familiar with both apparatus and pair-mate.
- Step 2: In Step 2 of the experiment, we moved the demonstrator rat to the opposite side of the screen partition from its observer, and food deprived the demonstrator for 24 hr to ensure that it ate when given opportunity to do so.
- Step 3: We then removed chow from the observer's side of the cage (in preparation for testing of the observer) and moved the demonstrator to an enclosure in a room separate from the observer where it fed for 30 min on one of two diets: either cocoa-flavored diet (Diet Coc) or cinnamon-flavored diet (Diet Cin).
- Step 4: Next, we returned the demonstrator to the observer's side of the cage and allowed demonstrator and observer to interact freely for 15 min.
- Step 5: Last, we removed the demonstrator from the experiment and provided the observer with 22-hr access to two weighed food-cups, one containing Diet Coc and the other Diet Cin.

At the end of the 22-hr test period, the experimenter weighed the two food cups and determined the percentage of each observer rat's total intake that was Diet Coc.

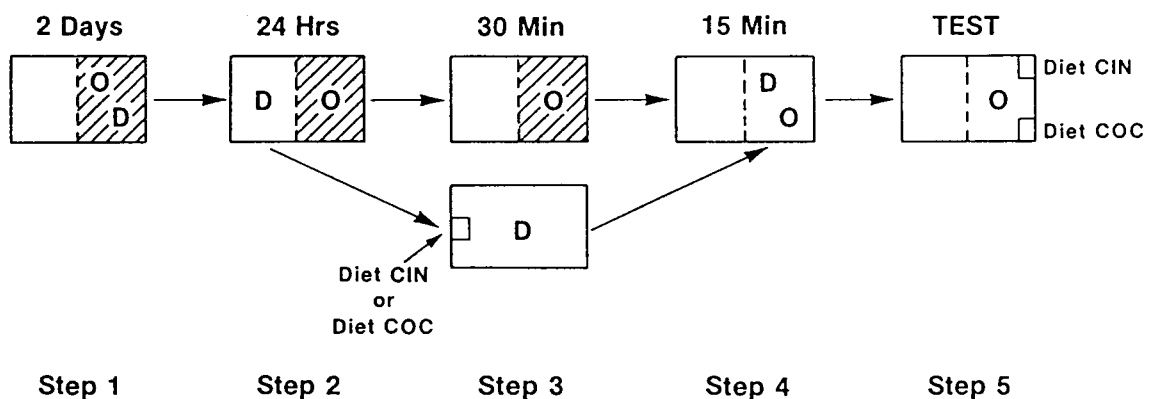


FIGURE 1. Schematic of the basic procedure of experiments. D = demonstrator. O = Observer. Diet Cin = cinnamon-flavored diet. Diet Coc = cocoa-flavored diet. Cross hatching indicates the presence of pellets of Purina chow in a cage. Reprinted by permission of Academic Press

As is evident in Figure 2, observer rats whose demonstrators had eaten Diet Coc ate a greater percentage of Diet Coc than did observer rats whose demonstrators had eaten Diet Cin (Galef and Wigmore 1983). Mice (*Mus domesticus*) exhibit similar social influences on their food preferences (Valsecchi and Galef 1989).

Such social effects on food preferences of rats are surprisingly long lasting. Figure 3 presents data from two groups of observer rats ($N = 12$ rats/group) that we offered a choice between Diet Cin and Diet Coc for $23\frac{1}{2}$ hr/day for 17 consecutive days. During the remaining $\frac{1}{2}$ -hr on each of the first 5 days of the experiment, each member of one group of 12 observer rats interacted with a demonstrator that had just eaten Diet Cin; the remaining 12 observers each interacted for $\frac{1}{2}$ hr/day with a demonstrator rat that had just eaten Diet Coc. As is evident from examination of Figure 3, observer rats exhibited effects of social interaction on their food preferences that lasted for at least 2 weeks (Galef 1989).

Social influences on food preference are also unexpectedly powerful. For example, social influence can reverse congenital taste preferences of rats (Galef 1989). For $23\frac{1}{2}$ hr/day, for 25 consecutive days, we offered subjects in both groups shown in Figure 4 a choice between Diet Coc and a diet (Diet Cay) flavored with cayenne pepper, a spice that rats find aversive. Subjects in

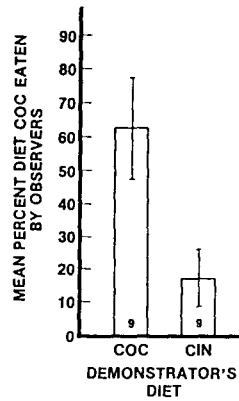


FIGURE 2. Mean amount of cocoa-flavored diet (Diet Coc) eaten by observer rats when given a choice between Diet Coc and cinnamon-flavored diet (Diet Cin) after interacting with demonstrator rats fed either Diet Cin or Diet Coc. Bars indicate ± 1 SEM. Reprinted by Permission of Academic Press.

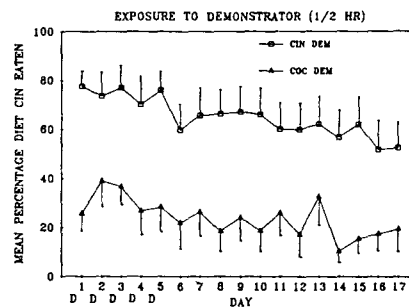


FIGURE 3. Mean amount of cinnamon-flavored diet (Diet Cin) eaten daily by observer rats offered a choice between Diet Cin and cocoa-flavored diet (Diet Coc) whose demonstrators ate either Diet Cin or Diet Coc. Observers interacted with their demonstrators on each day marked with a D. Bars indicate ± 1 SEM. Reprinted by permission of Academic Press.

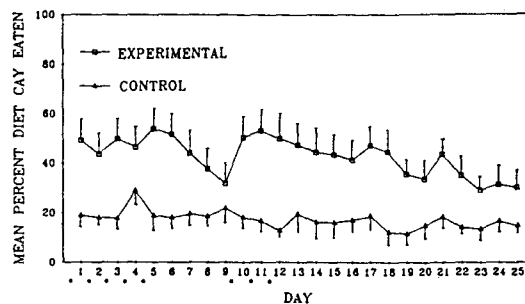


FIGURE 4. Mean amount of a piquant, cayenne-pepper-flavored diet (Diet Cay) eaten by subjects offered a choice between Diet Cay and cocoa-flavored diet and, on each day marked with an asterisk, either given Diet Cay to eat for 30 min/day (control group) or allowed to interact for 30 min/day with demonstrator rats that had eaten Diet Cay (experimental group). Bars indicate ± 1 SEM.

the control group were offered a bowl containing Diet Cay for the remaining ½ hr of each day marked with an asterisk on the abscissa of Figure 4; subjects in the experimental group interacted for ½ hr on each of the same days with a demonstrator rat that had been fed Diet Cay. As can be seen in Figure 4, experience of a food within the social context provided by the presence of a demonstrator rat had profound, prolonged effects on congenital flavor preferences that simple exposure to the same food did not.

Figure 5 presents a more detailed view of the effects of social influence on preference for Diet Cay. The surprising finding is that some subjects that interacted with demonstrators fed Diet Cay seem to have actually developed a liking for it (Galef 1989).

Socially acquired food preferences can also reverse the aversions that rats learn to the flavor of a food that they eat immediately before becoming ill (Galef 1986). We fed naïve observer rats a highly palatable diet (Diet NPT). We then made them ill by either injection of a moderate dose of lithium chloride (0.75% of body-weight of isotonic (0.13M) lithium chloride solution injected intraperitoneally) or injection with an equal volume of harmless, isotonic saline solution. Twenty-four hr after injection, we let one-half the subjects we had injected with lithium chloride interact for ½ hr with demonstrator rats that we had fed Diet NPT, the diet to which the subjects had learned an aversion. The remainder of the observers injected with lithium chloride interacted with a food bowl containing Diet NPT while subjects in the other group were interacting with demonstrators fed Diet NPT. Then we offered all observers a choice for 22 hr between Diet NPT, the diet to which they had learned an aversion, and a totally novel diet, Diet Coc (Galef 1986).

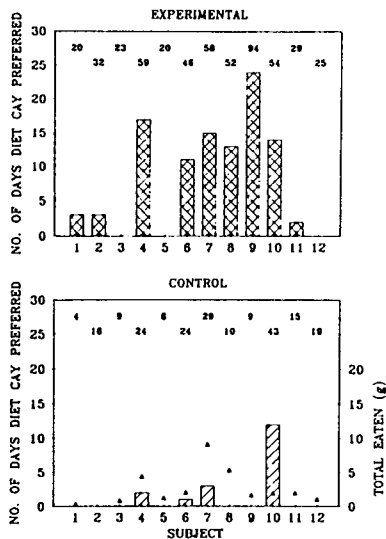


FIGURE 5. Number of days out of 25 that each subject in experimental and control conditions ate more cayenne-pepper-flavored Diet Cay than cocoa-flavored Diet Coc. Numbers above histograms = the mean percentage Diet Cay was eaten by observer rats across the twenty-five 23-hr periods of diet choice. Triangles in lower panel = the total amount of Diet Cay eaten by each control subject during eight 30-min periods in which Diet Cay was presented. Reprinted by permission of Academic Press.

As can be seen in Figure 6, observers that interacted with demonstrators acted as though they had never been poisoned at all. Interaction with demonstrator rats fed Diet NPT essentially obliterated a toxicosis-based learned aversion to Diet NPT.

Perhaps the most counter-intuitive result in the series of experiments that we conducted on social influences on food choice in rats concerns the behavior of observer rats that interact with sick or unconscious demonstrators. One might expect, on functional grounds, that an observer rat would avoid eating a food that it had learned that an obviously ill conspecific demonstrator had recently eaten. Yet in experiment after experiment, we have found (Galef et al. 1983, 1990), as have others (Grover et al. 1988), that naïve rats develop a preference for, not an aversion to, foods that they learn that unwell conspecifics have eaten.

Such preferences, learned by observer rats for foods eaten by unwell demonstrator rats, are worth mentioning because the repeated failure of rats in our experiments to communicate effectively about what foods to avoid eating suggests that the system of communication about foods we have explored evolved to facilitate rats' identification of safe, nutritious foods, not to facilitate their avoidance of toxins. This bias in the kind of information about foods transmitted from one animal to another suggests that finding foods may be as important a problem for rats as is avoiding toxins, though, during the last 2 or 3 decades, far more experimental work has been directed toward understanding poison avoidance than nutrient selection.

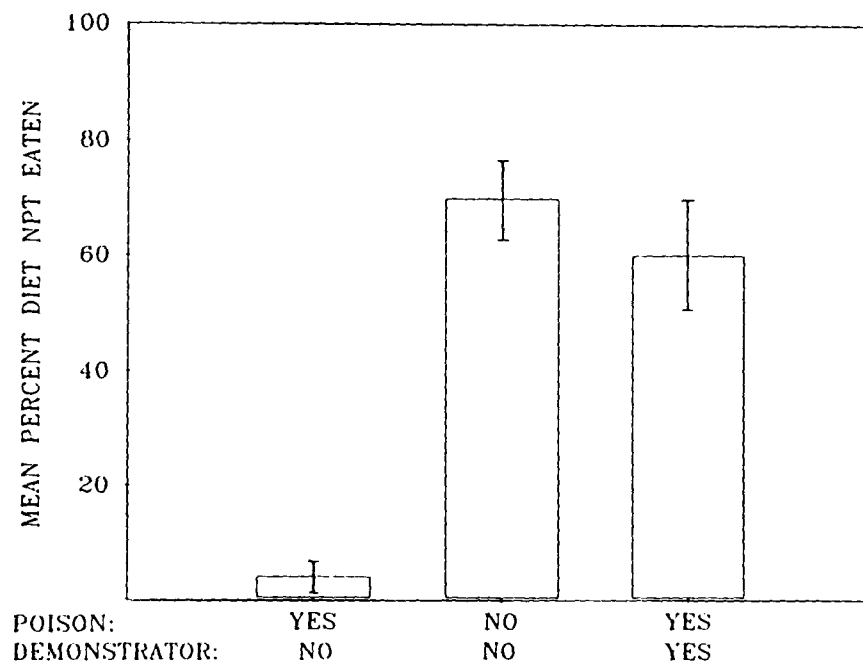


FIGURE 6. Mean percent Diet NPT eaten by observer rats offered a choice between Diet NPT and a cocoa-flavored diet after eating diet NPT and either being: (1) injected with saline solution, (2) injected with lithium chloride solution, or (3) injected with lithium chloride and then allowed to interact with two demonstrator rats that had eaten Diet NPT. Bars indicate ± 1 SEM.

The Mechanism

It is one thing to demonstrate that rats can communicate information to one another concerning diets eaten somewhere other than the place where communication occurs and that such communication biases subsequent diet selection by its recipients. It is quite another matter to determine the nature of the messages passing between rats that cause such socially induced changes in food preference.

We have developed several lines of evidence, each of which is consistent with the hypothesis that olfactory cues passing from demonstrator rats to their observers are sufficient to allow social induction of diet preference to occur (Galef and Wigmore 1983). Below, I describe two relevant experiments: first, if one renders an observer rat anosmic (unable to smell) before it interacts with its demonstrator, as can be seen in Figure 7, the observer fails to exhibit a preference for its demonstrator's diet during a subsequent 22-hr test. Control observer rats (observers whose nasal passages had been rinsed with saline solution) showed a significant tendency to eat the same diet that their respective demonstrators had eaten. Anosmic observer rats, those whose nasal passages had been rinsed with a zinc-sulfate solution that causes a transient anosmia, did not exhibit such a tendency (Galef and Wigmore 1983). Clearly, sensitivity to olfactory cues is necessary for information transfer from demonstrator to observer to occur. Second, humans, as well as rats, can tell what diet a rat has been eating using olfactory cues emitted by rats that have recently fed. If you feed ½-dozen rats Diet Coc and feed another ½-dozen rats Diet Cin, and then present all 12 rats (in random sequence) to a human observer who has been instructed to sniff the rats' breaths, he or she can tell with 85 to 90% accuracy which rat has eaten which diet; however, our human observers have not reported any resulting craving for the cinnamon- or cocoa-flavored rat diet.

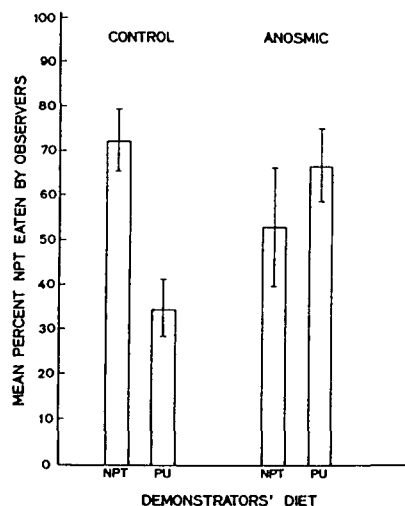


FIGURE 7. Mean percent Diet NPT eaten by intact control and anosmic observer rats offered a choice between Diet NPT and Purina chow (Diet Pur) after interacting with demonstrator rats fed either Diet NPT or Diet Pur. Bars indicate ± 1 SEM. Reprinted by Permission of the American Psychological Association.

It is, of course, not too surprising that an observer, either human or rodent, can tell what food a rat has recently eaten by smelling the rat's breath. The more difficult and more interesting question is why an observer rat, after determining that a conspecific has just eaten cinnamon-flavored food, should suddenly exhibit enhancement of its own desire to eat cinnamon-flavored food, or, conversely, why an observer rat after interacting with another of its species that has just eaten cocoa-flavored food should suddenly develop a liking for that food.

Norway rats, particularly wild Norway rats, are hesitant to eat unfamiliar foods (Barnett 1958, Galef 1970). Consequently, simple exposure to a food can, at least under some circumstances, enhance later preference for a preexposed food (Stetter et al. 1995). If rats are afraid to eat unfamiliar foods and if simple exposure to the smell of a food on a demonstrator rat increases the familiarity of an observer with that food, the effect of demonstrator rats on their observers' later diet preferences could be explained easily; demonstrator rats could be understood as simple, passive carriers of food odors. On this view, exposure of observer rats to food odors on their demonstrators overcomes the hesitancy of observers to eat an otherwise unfamiliar food, increasing preference for it.

However, the results of a series of studies carried out over the years offer no support for the hypothesis that changes in observer rats' diet preferences result from simple exposure of observer rats either to the smell or to the taste of the diet eaten by demonstrators. That is, simple exposure to diet-related cues is not, in itself, sufficient to produce alterations in observers' diet preferences—at least it has not done so in my work situations.

For example, when we gave one group of naïve rats access to Diet Cin for 30 min/day for 5 consecutive days and another group of rats access to Diet Coc for 30 min/day for 5 consecutive days, and offered both groups of rats a choice between Diet Cin and Diet Coc for the remaining 23½ hr of each day, as can be seen in Figure 8, there was no effect of this ½-hr daily exposure to a diet on subjects' diet preferences. When we then gave the same rats 30 min/day to interact with demonstrator rats fed either Diet Cin or Diet Coc, we saw massive effects on the diet choices of their observers; the observers preferred to eat the food that their respective demonstrators had eaten. Observers exhibited an enhanced preference for their respective demonstrators' diets despite the fact that the observers had been living on Diet Cin and Diet Coc for 7 days before exposure to their demonstrators and were, therefore, completely familiar with both diets (Galef 1989).

The results presented in Figure 8 suggest that changes in observer diet preference require more than simple exposure to a diet; changes in the diet preferences of observers require exposure to diet-related cues in the social context provided by the presence of a demonstrator. If, in fact, changes in observers' diet preferences depend on exposure to diet-related cues in a social context, we are left with two important questions: (1) what is the source of the diet-related cues that are emitted by demonstrators and detected by their observers that permit observers to know what foods their respective demonstrators ate, and (2) what is the source of the contextual cues, the social cues emerging from a demonstrator, that render exposure to diet-related cues effective in altering observers' later diet preferences?

The answer to the first question is fairly simple. We have found that both particles of food clinging to the fur and vibrissae of a rat and the odor of food escaping from the gastrointestinal

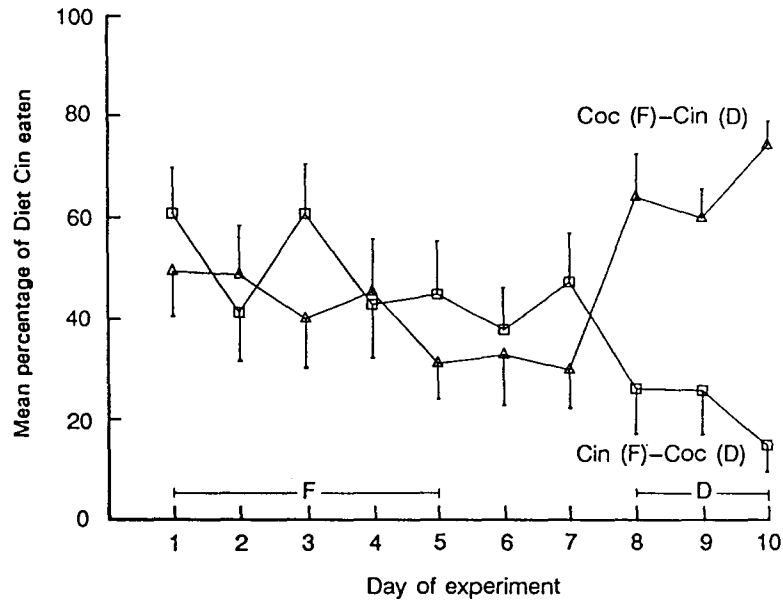


FIGURE 8. Mean percent of cinnamon-flavored diet (Diet Cin) eaten daily by observer rats offered a choice between Diet Cin and cocoa-flavored diet (Diet Coc) for 23½ hr/day and exposed to either Diet Cin or Diet Coc for 30 min/day on each of the 5 days marked with an F on the abscissa and exposed to a demonstrator rat fed either Diet Cin or Diet Coc on each of the 3 days marked with a D along the abscissa. Bars indicate ± 1 SEM. Reprinted by permission Academic Press.

tract of recently fed rats are sufficient to allow observer rats to identify the food that their respective demonstrators have eaten (Galef et al. 1985, Galef and Stein 1985).

The answer to the second question is more interesting. The method we used to answer it was similar to that we used in the very first experiment described above (see Figure 1), except in the ways in which we exposed demonstrators to their respective diets and in the conditions under which demonstrators and observers interacted.

When a demonstrator and observer interacted, the demonstrator was anesthetized and held in a wire-mesh tube inserted into a cardboard bucket like that used in certain fast-food franchises. An observer was placed in the body of the bucket and allowed to interact for ½ hr with its demonstrator (see Figure 9).

We exposed demonstrators to diets in a number of different ways:

- (1) Each powdered-face demonstrator was anesthetized and its face rolled in either Diet Cin or Diet Coc. It was then placed in a wire mesh tube and presented to an observer restrained in the cardboard bucket. As can be seen in Figure 10, powdered-face demonstrators were very effective in altering their observers' diet preferences, so our procedures haven't disrupted communication between demonstrators and their observers (It is worth noting that these unconscious and, therefore, obviously unwell demonstrators were very effective in inducing a preference for the flavored diet with which they were associated).

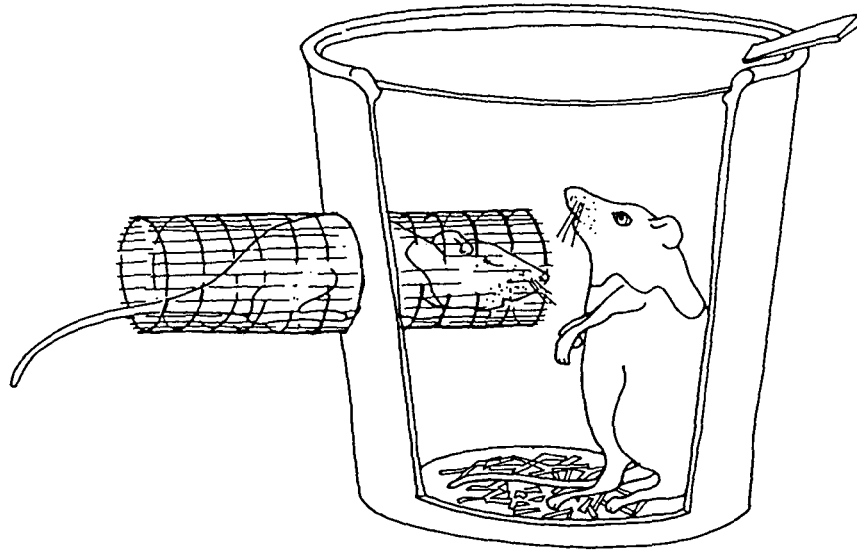


FIGURE 9. Illustration of the cardboard-bucket apparatus showing an anesthetized demonstrator rat in the wire-mesh tube inserted into the bucket and an observer rat in the bucket itself. Reprinted by permission of the American Psychological Association.

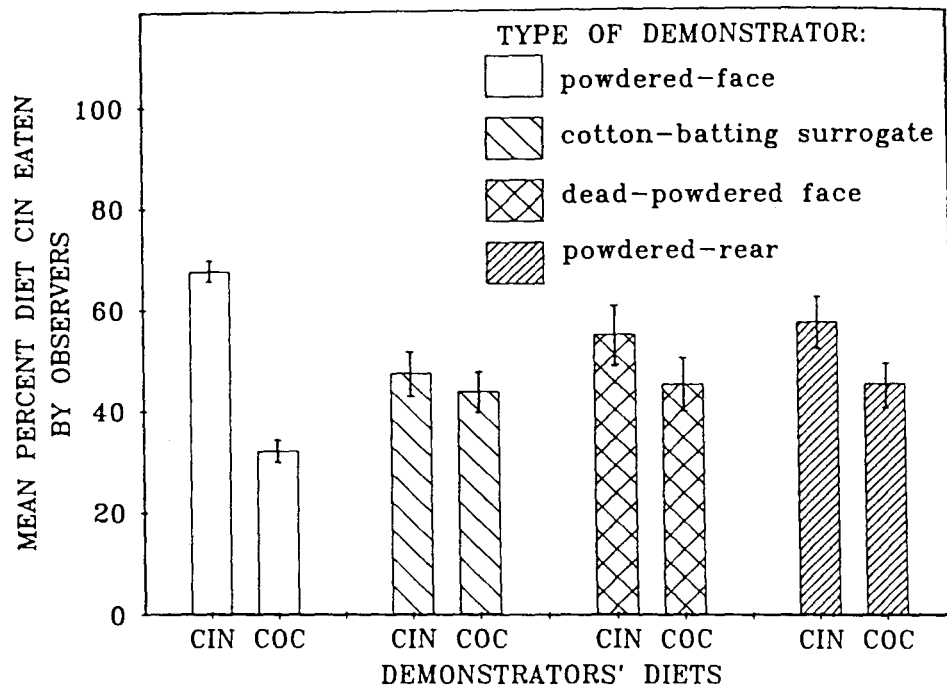


FIGURE 10. Mean amount of cinnamon-flavored diet (Diet Cin) eaten by observer rats offered a choice between Diet Cin and cocoa-flavored diet (Diet Coc) after interacting with powdered-face demonstrators; powdered-rear demonstrators; dead, powdered-face demonstrators; or surrogate demonstrators that had been brushed with either Diet Cin or Diet Coc. Bars indicate ± 1 SEM.

- (2) Surrogate demonstrators were rat-sized lengths of surgical gauze stuffed with cotton-battling. One end of each surrogate was powdered with either Diet Cin or Diet Coc, then placed in a wire-mesh tube and presented to observers in the apparatus.
- (3) Dead, powdered-face demonstrators were sacrificed by anesthetic overdose, rather than simply anesthetized, and were then treated just like powdered-face demonstrators.
- (4) Powdered-rear demonstrators were anesthetized and their rear-ends (rather than their head ends) were rolled in either Diet Cin or Diet Coc. They were then put into wire-mesh tubes and the tubes inserted into the bucket with the rats' rear-ends intruding into the bucket and their heads outside of it.

As can be seen in Figure 10, observer rats that were exposed to surrogates did not exhibit a preference for the particular diet with which their respective surrogates had been powdered, reinforcing the point made above that mere exposure to a diet does not enhance preference for it. A diet has to be experienced by an observer rat in the context provided by the presence of another of its species if preference for that diet is going to be enhanced.

Observers assigned to the powdered-face condition exhibited significantly greater influence of demonstrators on their food preferences than did observers assigned to the dead, powdered-face condition, and demonstrators in the powdered-face condition also had significantly greater influence on observers than did demonstrators in the powdered-rear condition. What all this tells us is that the most potent contextual cues rendering a demonstrator's diet attractive to an observer emerge from the anterior of live rats (Galef and Stein 1985).

One obvious difference between live, anesthetized rats (that emit effective contextual cues) and recently sacrificed rats (that do not emit effective contextual cues) is that live rats are breathing while dead rats are not. Similarly, the anterior end of a live rat emits rat breath, while their posterior end does not. Consequently, it seemed reasonable to ask whether there might be substances present in rat breath that provide the contextual cues that make diet-identifying cues that are emitted by demonstrator rats effective in changing the diet preferences of their observers.

Because rats breathe only through their noses (not through their mouths), by comparing the chemical contents of samples of air taken from the noses of rats with the chemical contents of samples of air taken from their mouths, we could determine the chemical composition of rats' breath.

Figure 11 presents the results of some mass spectrometry of rats' breath carried out in collaboration with J. R. Mason and George Preti at the Monell Chemical Senses Center (Galef et al. 1988). The lowest panel in the figure shows a mass spectrogram of sulfur compounds in rat breath; and in the two upper panels, the computer matches the two largest peaks in the spectrogram with those in the lowest panel: carbonyl sulfide and carbon disulfide. Carbonyl sulfide, is a gas at room temperature and pressure and is, therefore, difficult to work with. Carbon disulfide (CS₂) is a volatile liquid and would be easier to use.

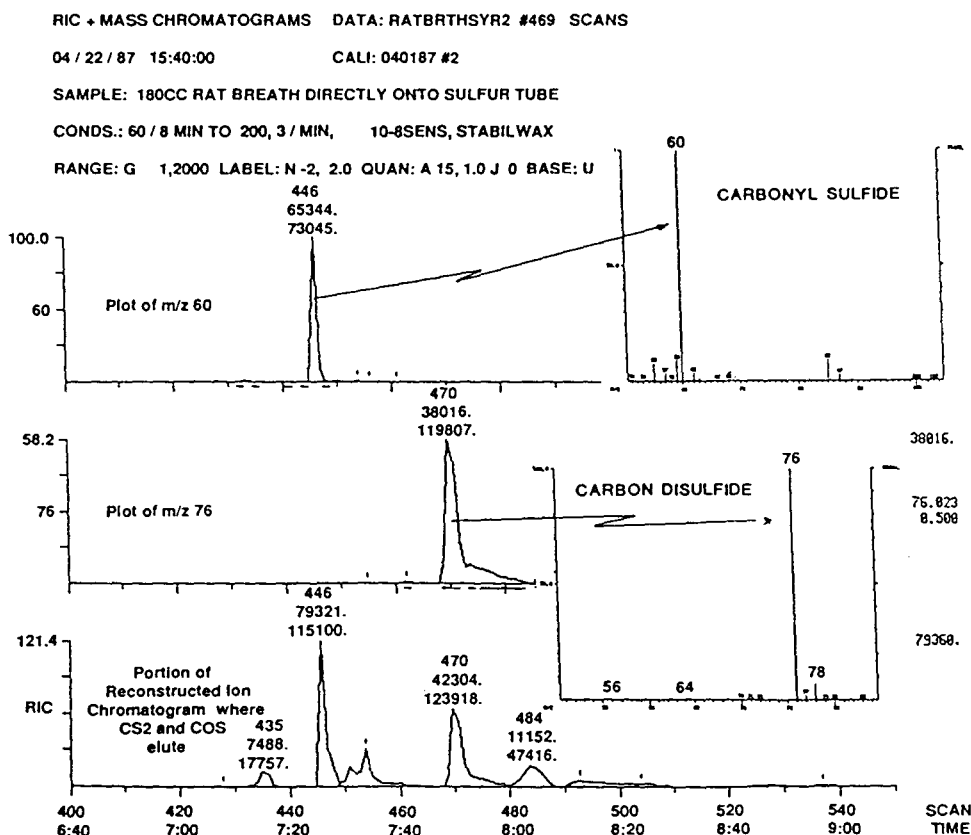


FIGURE 11. Reconstructed ion chromatogram of rat breath showing molecular ions for carbonyl sulfide (COS) and carbon disulfide (CS₂). Reprinted by permission of Pergamon Press.

I won't describe the relevant experiments in detail here, but as can be seen in Figure 12, we have found that by adding a few drops of a very dilute solution of CS₂ in water (10 ppm) to a cotton-batting surrogate rat powdered with food, we were able to make that surrogate as effective as an anesthetized demonstrator rat in altering observers' food preferences. Observers exhibited substantial enhancement of their intake of cocoa- or cinnamon-flavored diet following exposure to a cocoa- or cinnamon-flavored-diet, powdered cotton-batting surrogate that had been moistened with CS₂ solution, but not following exposure to a similar surrogate that had been moistened with a similar quantity of distilled water. So, CS₂ appears to be an important component of the context that makes demonstrator rats effective in altering the food preferences of their observers (Galef et al. 1988).

A RODENT ATTRACTANT

In field tests, J. R. Mason, Jay Bean and I (Mason et al. 1989) found that placing an aqueous solution of CS₂ near a sample of food substantially increased intake of that food relative to control

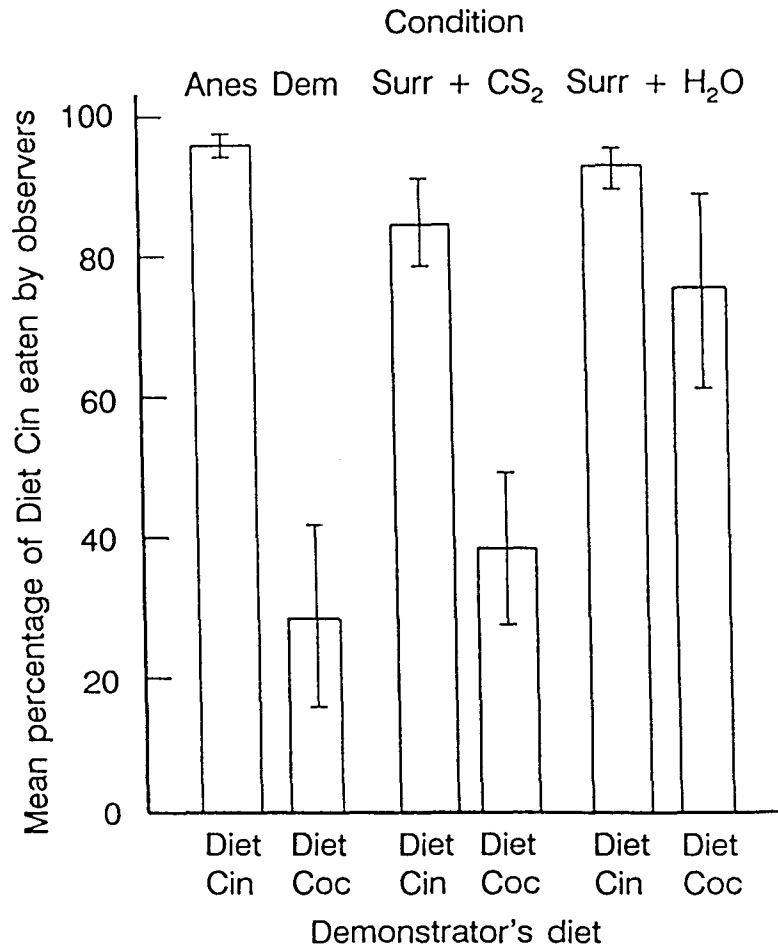


FIGURE 12. Mean amount of cinnamon-flavored diet (Diet Cin) eaten by observer rats offered a choice between Diet Cin and cocoa-flavored diet (Diet Coc) after interacting with either an anesthetized demonstrator rat, a surrogate rat moistened with distilled water, or a surrogate rat moistened with a dilute solution of carbon disulfide, each of which had been brushed with either Diet Cin or Diet Coc. Bars indicate ± 1 SEM. Reprinted by permission of Pergamon Press.

samples of food without CS₂ nearby. As can be seen in Figure 13, over 6 nights, three colonies of Norway rats living in a pig barn, a livestock feeding pen, and a pheasant holding pen each ate three or more times as much from baiting stations containing 10 ppm CS₂ solution in a vial closed with a wick than they ate from unscented baiting stations.

Similarly, T. Miller, working in the laboratory, found that adding starch xanthate (a substance which slowly releases CS₂) to Environmental Protection Agency challenge diet substantially increased intake of that diet by groups of rats (T. Miller, pers. commun.). Mice also ate more of a bait associated with CS₂ than of the same bait in the absence of CS₂ (Bean et al. 1988). So there is evidence consistent with the view that CS₂, the same chemical that is active in intraspecific communication about foods by rodents, can be used as an enhancer of rodent baits, though there are practical problems associated with using CS₂ on a large scale in rodent control.

The results of such studies were unequivocal; on almost 90% of trials naïve rats entered the same arm of the maze as had their respective leaders. If, on the other hand, a leader rat did not discover food in the arm of the maze it entered, it did not deposit a trail that was attractive to other rats, and rats placed in the start box of the maze after an unfed leader had been removed from it entered equally the two arms of the maze (the one the leader had entered and its alternative) (Galef and Buckley 1996).

Our observations of the behavior of leader rats in the maze failed to reveal any overt scent-marking behavior on their part, and inspection of the floor of the maze after a leader had traversed it revealed what appeared to be urine along its length. We, therefore, hypothesized that the attractive substance or substances in the trails that leader rats deposited on their way back from a feeding site were carried in their urine.

We have collected samples of urine from rats held in metabolism cages and painted trails along the floor of the maze into one or the other of its arms and found that such trails were as attractive to naïve rats as were the trails that leader rats deposited as they traveled from feeding site to start box in the maze. Although we have not yet been successful in using aqueous solutions of the material deposited by rats on the floor of the maze to lay trails that are attractive to their fellows, we are continuing in our efforts to extract the active chemical directly from these trails.

We hope someday to be able to ship to our colleagues at the Monell Chemical Senses Center for analysis a container of substance taken from the floor of a maze that is attractive to rats. With luck, we may one day be able to paint chemical trails on the substrate that will lead rats directly to poison baits.

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