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OLFACTORY COMMUNICATIONS ABOUT FOODS AMONG RATS: A REVIEW OF RECENT FINDINGS

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ABSTRACT We review recent studies of social influence on the development of food preferences by Norway rats. These studies provide evidence that exposing an observer rat to food odors carried on the breath of a demonstrator rat produces a reliable increase in the observer's preference for the foods that its demonstrator ate. Such social learning provides a plausible explanation of how weanling rats living in natural environments learn to select nutritionally valuable foods to eat.

OVERVIEW (1982-1985)

The Phenomenon

In 1982, Steven Wigmore and I, following a lead provided by Barbara Strupp (See Strupp and Levitsky, 1984; Galef, 1991b), discovered that, after a naive rat (an observer) interacted with a recently fed conspecific (a demonstrator), the observer exhibited a substantial enhancement of its preference for whatever food its demonstrator had eaten (Galef and Wigmore, 1983; Posadas-Andrews and Roper, 1983). Such social influence on diet selection by rats was surprisingly robust (Galef et al., 1984); it was found in a variety of different laboratory situations, in rats of all ages, of both sexes and of several different strains (Galef et al., 1984; Richard et al., 1987).

The Analysis

Results of several experiments are consistent with the view that observer rats use olfactory cues emitted by their respective demonstrators to identify the foods that those demonstrators have eaten (Galef and Wigmore, 1983). For example, anosmic observer rats (i.e. those whose sense of smell had been blocked) did not develop a preference for foods eaten by their demonstrators in situations where intact control rats did develop such a preference (for further evidence, see Galef and Wigmore, 1983).

Results of further experiments indicated that, during periods of social interaction, observer rats were experiencing more than simple exposure to the odors of foods that their respective demonstrators had eaten (Galef et al., 1985). Allowing observer rats either to smell or to eat a food did not enhance their preferences for that food, while allowing observer rats to interact with

demonstrator rats that had eaten the same food did enhance observers' preferences for it (Galef and Stein, 1985; Galef et al., 1985).

We interpreted such findings as suggesting that the olfactory messages passing from demonstrator rats to their observers, that result in changes in observers' food preferences, have two components: first, a diet-identifying component (the smell of a food, which allows an observer rat to identify the food that its demonstrator has eaten) and, second, a contextual component (an odor associated with rats, which renders the diet-identifying component of the olfactory message emitted by demonstrators effective in altering observers' later food choices).

We found that the diet-identifying component could be provided either by portions of food introduced directly into demonstrators' stomachs or by particles of food clinging to the fur and vibrissae of demonstrators (Galef et al., 1985). The contextual component appeared to emerge from the anterior of living, anesthetized rats, not from either the posterior of living, anesthetized rats or from the anterior of rats recently sacrificed by anesthetic overdose (Galef and Stein, 1985).

This concentration of effective contextual cues at the anterior of living rats led us to hypothesize that the contextual cues that enhance rats' preferences for foods eaten by their demonstrators might be contained in rat breath, a possibility to which I shall return in the penultimate section of the present chapter.

RECENT DEVELOPMENTS (1985-1991)

Magnitude of Social Effects on Diet Choice by Norway Rats

The results of the experiments summarized above demonstrate that socially acquired information can modify the food choices of Norway rats. However, these experiments provide no insight into the magnitude of such social influences on food preference, relative to other determinants of food choice.

In the present section, I describe two experiments (from a series of four) concerned with the relative strength of social interactions in guiding the food choices of rats. In brief, we found (Galef, 1986c) that social influence could reverse food aversions based either on taste-toxicosis conditioning or on unpalatability (as described below) and could reduce food preferences based on either sodium appetite or handling time (see Galef, 1986c).

Effects of Social Information on Learned Aversions

A rat that has eaten an unfamiliar food and subsequently suffered gastrointestinal upset, when subsequently offered that food in a choice situation, avoids eating it (Garcia and Hankins, 1977). We taught naive rats in each of six experimental groups an aversion to a highly palatable food (Diet NPT) by

injecting the rats with lithium chloride (LiCl) solution immediately after they had eaten Diet NPT for the first time. After these rats had recovered from toxicosis, we allowed them to interact either for 1/2 hr or for 1 hr with either: (1) a bowl containing Diet NPT, (2) a single demonstrator that had eaten Diet NPT, or (3) two demonstrator rats in succession, each of which had eaten Diet NPT. The observer rats were then given a choice, for 22 hr, between Diet NPT and a second food (Galef, 1986c).

As can be seen in Figure 1, interaction with demonstrator rats that had eaten Diet NPT caused many observer rats that had learned an aversion to Diet NPT to abandon that aversion. In fact, half the observers in those experimental groups whose members interacted with two demonstrators (Group 2-Dem, LiCl in Figure 1) exhibited food choices similar to those of subjects in control groups (Groups Bowl, Saline) that had been injected with saline solution after eating Diet NPT for the first time and were then allowed to interact with a bowl containing Diet NPT for either 1/2 or 1 hr immediately before they were given the 22-hr choice between Diet NPT and an unfamiliar diet. Social influence can significantly attenuate toxicosis-induced aversions (See also Galef et al., 1990).

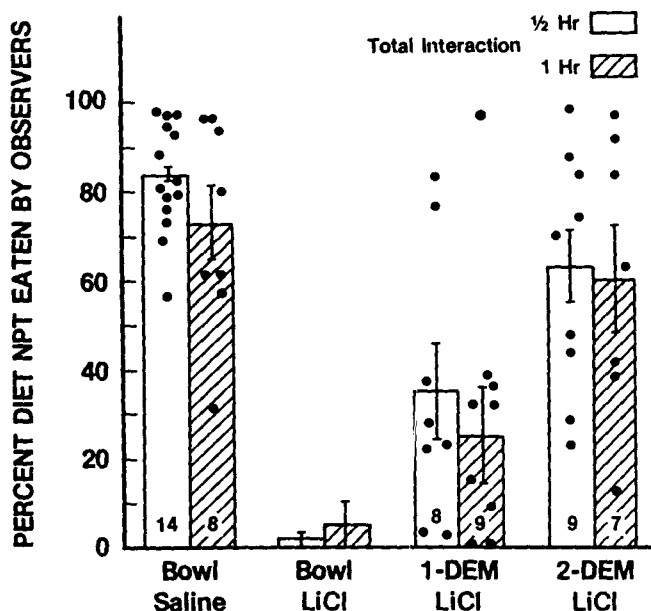


Figure 1. Mean amount of Diet NPT eaten by observers, as a percentage of the total amount that they ate during testing (Galef, 1986c).

Effects of Social Interaction on Ingestion of Unpalatable Foods

Choices among foods are influenced by the relative palatabilities of available items and relative palatabilities are normally quite stable throughout the lives of animals. For example, Rozin et al. (1979) were unable to induce rats to increase their preferences for a cayenne-pepper-flavored food even after 11 months of continuous, forced intake of it.

We attempted to induce lasting preferences in rats for a cayenne-pepper-flavored food (Diet Cay) by exposing each rat in an experimental group (for 1/2 hr/day for 5 consecutive days) to a demonstrator rat that had been required to eat Diet Cay (Galef, 1989). For the remaining 23 1/2 hr of each of the 25 days of the experiment, rats both in this experimental group and in a control group (the members of which were exposed to a bowl containing Diet Cay, while subjects in the experimental group were exposed to a demonstrator fed Diet Cay) were offered a choice between Diet Cay and a cocoa-flavored diet.

As can be seen in Figure 2, subjects in the experimental group (those that had interacted with a demonstrator rat fed Diet Cay) exhibited enhanced intake of Diet Cay. In fact, 5 of the 12 subjects in the experimental group ate more Diet Cay than cocoa-flavored diet during the 25 days of the experiment; none of the 12 subjects in the control group did so (Galef, 1989).

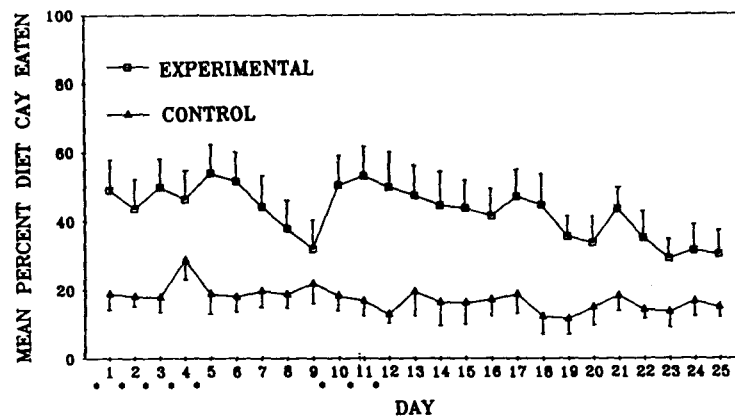


Figure 2. Mean amount of cayenne-pepper-flavoured diet eaten by subjects that either were given Diet Cay to eat for 30 min/day (▲) or interacted for 30 min/day with a demonstrator rat that had eaten Diet Cay (■) (Galef, 1989).

Complexities in the World Outside the Laboratory

In all of the experiments described both above and in previous reviews (Galef, 1986a; 1988), observer rats interacted with demonstrator rats that had relatively simple recent histories of food intake: (1) each demonstrator rat with which an observer interacted had eaten only a single food during the 24-hr period before interaction took place, and (2) any observer rat that interacted with more than one demonstrator interacted with demonstrators that had all eaten the same food.

It is reasonable to suppose that, in the world outside the laboratory: (1) free-living Norway rats often eat several different foods before returning to their burrows to interact with colony mates, (2) interactions among rats may often involve individuals each of which has recently eaten several different foods, (3) over days or weeks an individual rat may interact with many others that have each been eating different foods. Thus, in natural circumstances, a rat interacting with its fellows is likely to be subjected to an extended series of complex, food-related, olfactory messages. It is, therefore, important to know whether individual rats can extract usable information from complex food-related signals of a kind that they would be likely to encounter in the natural world (Galef, Attenborough and Whiskin, 1990; Galef, 1991a; Galef and Whiskin, 1992).

When demonstrators eat complex diets. My coworkers and I have carried out a number of experiments in which we varied the complexity of foods that were fed to demonstrator rats before the demonstrators interacted with their observers. We then looked to see whether observers could extract useful information from demonstrators that had eaten several different foods before they interacted with their respective observers (Galef, 1990, 1991a; Galef et al., 1990; Galef and Whiskin, 1992). Rather than recount the history of our explorations of communications concerning complex foods, I'll describe here only the most complex of the situations that we have examined to date (Galef and Whiskin, 1992).

Food deprived rats were each fed, for 1 hr, powdered rat chow to which had been added one of two combinations of four spices: either Combination A - cinnamon, anise, thyme and cloves - or Combination B: cocoa, marjoram, cumin and rosemary. Next, individual rats that had eaten Combination A were allowed to interact for 1/2 hr with individual rats that had eaten Combination B. Finally, each rat was offered a choice, for 22 hr, between one of four pairs of flavored diets: either (1) cinnamon-flavored vs. cocoa-flavored diet, (2) anise-flavored vs. marjoram-flavored diet, (3) thyme-flavored vs. cumin-flavored diet or (4) clove-flavored vs. rosemary-flavored diet. One flavor in each of the four pairs was a constituent of Combination A; the other flavor was a constituent of Combination B.

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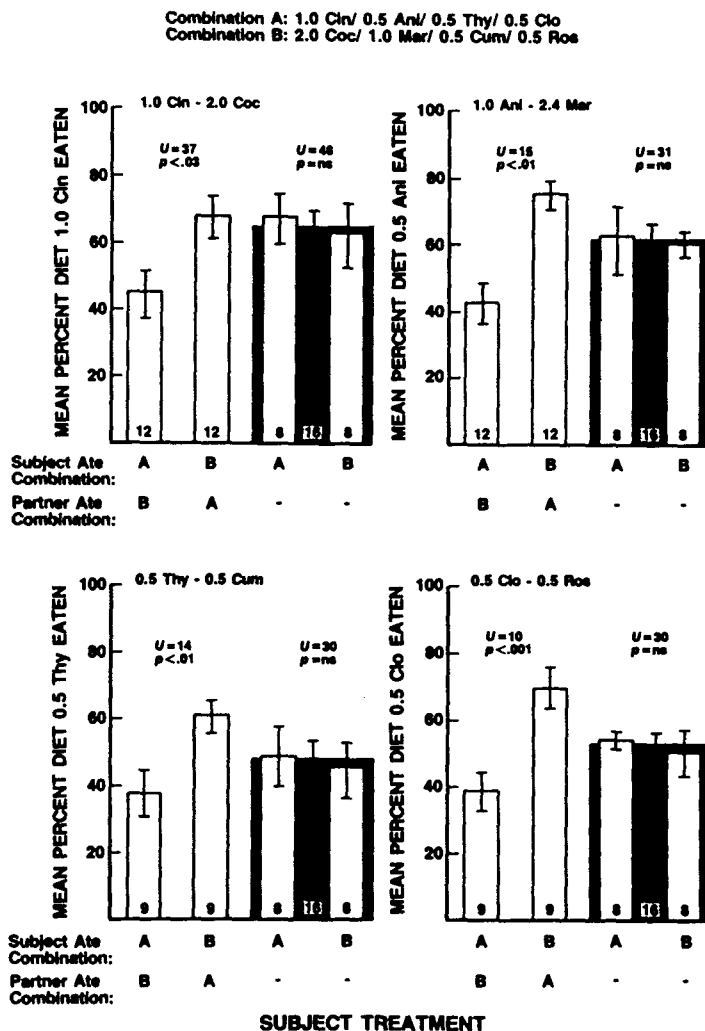


Figure 3. Each of the four panels shows the percentage of either Diet 1.0 Cin, Diet 0.5 Ani, Diet 0.5 Thy, or Diet 0.5 Clo eaten by subjects. The flavorants present in Combinations A and B are shown above the figure; the choice of diets offered to each group of subject is indicated by the floating title above each panel; the shaded histograms indicate the combined mean for subjects in both control groups offered the same choice of diets; the numbers in each histogram = n/group. Flags = ± 1 SEM (Galef and Whiskin, 1992).

As can be seen in Figure 3, when offered a choice between any of the four pairs of flavored diets, subjects preferred the diet containing a flavor that their respective partners had eaten to the diet containing a flavor that they themselves had eaten. As can also be seen in Figure 3, subjects in control

groups (subjects that ate a four-flavored diet and did not interact with a partner) did not exhibit comparable patterns of preference (Galef and Whiskin, 1992). We concluded that observers' could develop preferences for the flavors that their partners had eaten, even when their partners had eaten quite complex diets.

When observers interact with a series of demonstrators. Observer rats can respond not only to complex single messages, but also to a succession of simple messages received from a series of demonstrators (Galef et al., 1990). On each of nine occasions spread over 23 days, observer rats in an experimental group interacted for 1/2 hr with a demonstrator rat that had just eaten a diet unfamiliar to the observer. Observers in a control group interacted with a demonstrator rat fed the diet on which both demonstrators and observers had been maintained throughout life.

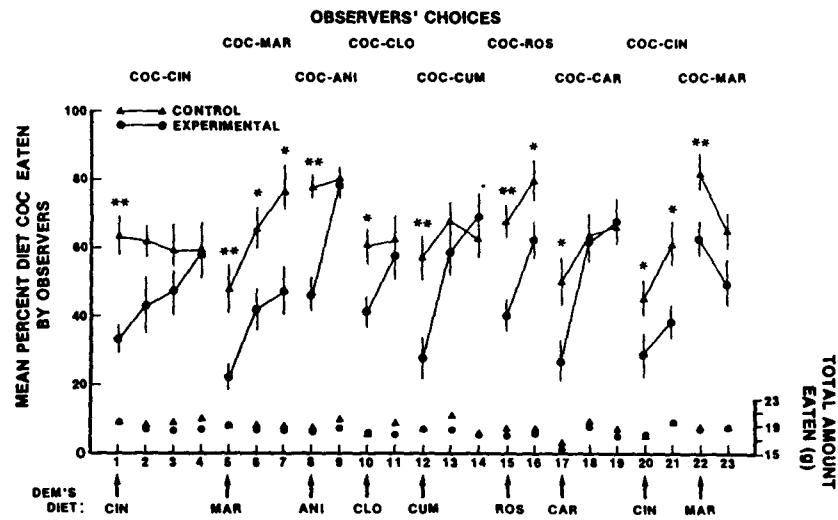


Figure 4. Mean percentage of Diet Coc eaten and total amount eaten by observers in control and experimental groups during daily 23½-hr tests. Pairs of diets shown at the top of the figure indicate the choice offered to observers on each day. Diets shown at the bottom of the figure indicate foods presented to demonstrators on days indicated by the vertical arrows. *p < .05. **p < .01. CIN = cinnamon diet; MAR = marjoram diet; ANI = anise diet; CLO = clove diet; CUM = cumin diet; ROS = rosemary diet, and CAR = cardamon diet (Galef et al., 1990).

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Figure 4 shows the days on which demonstrators and observers interacted, the diets fed to demonstrators in the experimental group before they interacted with their observers, and the food choices given to all subjects for 23 1/2 hr on each of the 23 days of the experiment. As can be seen in Figure 4, on each of the 9 days of the experiment that observer rats interacted with demonstrators, observers in the experimental group exhibited a significant enhancement of their intake of each of the foods that their respective demonstrators had eaten.

Limitations on Olfactory Communications about Distant Diets

When I describe our research on social transmission of diet preference to an audience, whether of psychologists or biologists, one of the first questions that I am invariably asked is "If a naive observer rat interacts with a sick demonstrator rat that has eaten an unfamiliar food will the observer learn an aversion to the food that its sick demonstrator ate?"

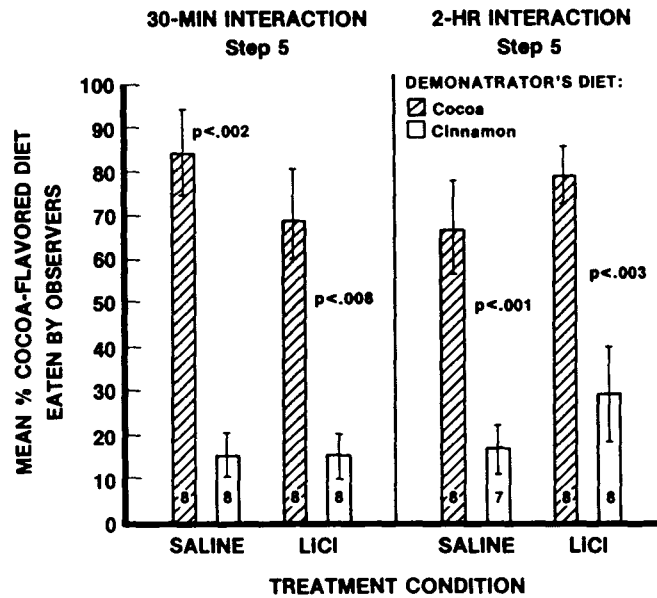


Figure 5. Mean amount of Diet Coc eaten as a percentage of total intake during testing by observers that ate either Diet Cin or Diet Coc and were injected with either saline or lithium chloride (Galef et al., 1983).

The question is a good one, and the questioner has every reason to expect a positive response. We have shown that an observer rat can determine what food a demonstrator rat ate (Galef and Wigmore, 1983) and a number of investigators have reported that signals emitted by ill rats can serve as unconditional stimuli in a taste-aversion-learning paradigm (Coombes et al., 1980; Lavin et al., 1980; Bond, 1982; Stierhoff and Lavin, 1982, but see Gemberling, 1984). Consequently, it is reasonable to expect that observer rats would learn to avoid foods eaten by sick demonstrators.

My coworkers and I were, therefore, surprised to find (as audiences are surprised to hear) that, instead of learning aversions to foods that sick demonstrators have eaten, observer rats actually exhibit enhanced preferences for such foods (Galef et al., 1983; Galef et al., 1990). As can be seen in Figure 5, observer rats that interacted for either 30 min or for 2 hr with demonstrators that had been fed either cinnamon- or cocoa-flavored diet and had then been made ill by injection with LiCl solution, exhibited socially enhanced preferences for (not aversions to) the foods that their respective demonstrators ate (Galef et al., 1983).

Indeed, several years of experimentation, both in our laboratory and elsewhere (Galef et al., 1983; Grover et al., 1988; Galef et al., 1990), have produced no evidence consistent with the view that responses of observer rats to food-identifying signals emitted by their respective demonstrators are modified by the state of health of those demonstrators.

Degrees of Plasticity in Observers' Responses to Demonstrators

Although the responses of observer rats to diet identifying cues emitted by demonstrator rats are not affected by the state of health of demonstrators, responses of observer rats to messages from demonstrators appear to be affected by the state of health of the observers themselves. We have found that the food choices of protein-deprived observer rats are more profoundly influenced by foods eaten by demonstrators than are the food choices of protein-replete observer rats. Using the enclosure depicted in Figure 6, Galef et al. (1991) offered both protein-deficient and protein-replete juvenile rats a choice among four different-flavored, protein-deficient diets.

As can be seen in Figure 7, during the 7 days of the experiment, protein-deprived observers with demonstrators ate more of the nutmeg-flavored diet than their demonstrators were eating than did protein-replete observers with demonstrators. On the other hand, protein-deprived and protein-replete observers without demonstrators ate equal amounts of nutmeg-flavored diet. We concluded that protein deprivation of observers increased the influence that demonstrators had on the food choices of their observers.

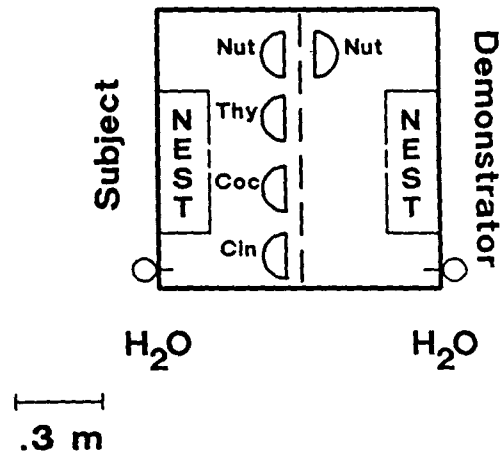


Figure 6. Overhead schematic of apparatus used to study intakes of observer rats self selecting among four diets (Beck and Galef, 1989).

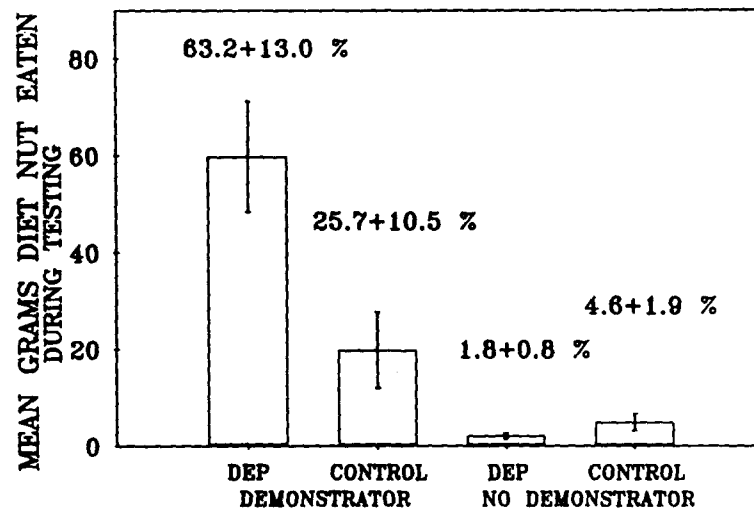


Figure 7. Mean (\pm SE) total amount of Diet Nut eaten during 7 days of testing by protein-deprived and replete (control) subjects with and without demonstrators (Dems). Numbers above histograms indicate the mean (\pm SE) percent Diet Nut eaten by subjects in each group (Galef et al. 1992).

Functions of Social Learning about Food

It's one thing to know that olfactory messages passing from one rat (Galef and Wigmore, 1983) or mouse (Valsecchi and Galef, 1989) to another can alter the later food preferences of rodents. It's quite another matter to understand how such socially induced changes in food choice might facilitate development of adaptive feeding patterns in rodents living outside the laboratory. In the present section, I review several experiments the results of which suggest that olfactory communications about foods help Norway rats to decide what foods to eat, what potential foods not to eat and where to go to find food.

Learning what to eat. Although individual rats can sometimes learn to feed on a single nutritionally adequate diet embedded in an array of nutrient-deficient diets (Richter et al., 1938; Rozin, 1969; Galef and Beck, 1990), it is relatively easy to create situations in which individual rats have great difficulty in focusing feeding on the sole adequate food in an array of foods (Beck and Galef, 1989; Galef et al., 1991). One need only: (1) provide subjects with four or more foods to choose among, (2) make the nutritionally adequate food the least palatable food in the array presented to subjects and (3) make sure that the nutrient that is present only in the nutritionally adequate food cannot be detected directly by rats (as, for example, salt can be). In such situations individual rats will often fail to self select the adequate food in the array presented to them.

Beck and I (Beck and Galef, 1989) placed individual rats in enclosures containing three protein-deficient foods (Diet Cin, Coc and Thy) and a single, relatively unpalatable food (Diet HP-Nut) containing adequate protein. Each subject was either alone in its enclosure or shared its enclosure with a conspecific demonstrator or demonstrators that had been trained both to eat the protein-rich food and to avoid eating the three, protein-deficient alternatives. As can be seen in Figure 8, observer rats with trained demonstrators in their enclosures were able to grow rapidly, while rats in isolation failed to thrive in the experimental situation.

Learning what not to eat. The ability to use conspecifics as sources of information about safe foods might be particularly helpful to individuals that had eaten several different unfamiliar foods in succession (as a naive weanling might) before falling ill from toxicosis. The problem facing such an individual would be to determine which of the several foods it had eaten had caused its illness.

Foods that conspecifics are eating are probably not noxious. If substances others were eating were noxious, then those that ate them once probably would have learned not to do so again. Thus, information acquired from others of one's social group concerning the foods that they are eating would be of potential value to those trying to avoid ingesting toxins.

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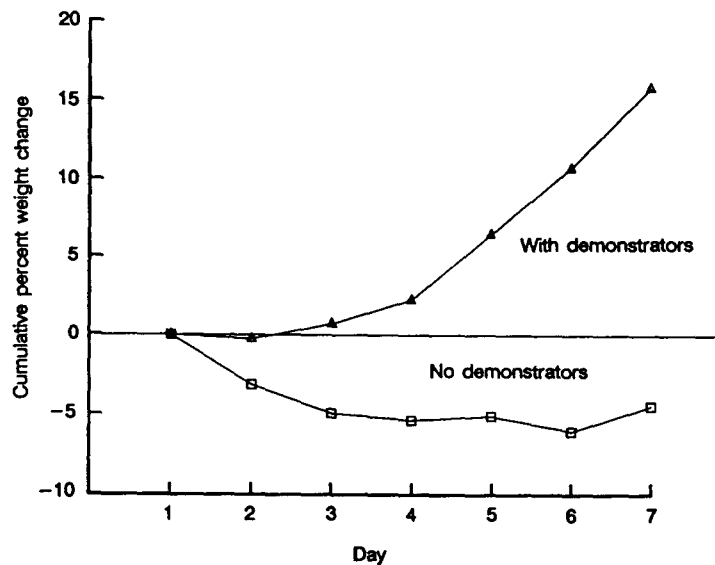


Figure 8. Mean cumulative percentage weight change of subjects during 7 days of testing (Beck and Galef, 1989).

I, first, fed demonstrator rats one of two foods, either cocoa-flavored diet (Diet Coc) or cinnamon-flavored diet (Diet Cin) (b) next, allowed each demonstrator to interact with a naive observer, (c) then, fed observers Diets Cin and Coc in succession for 15 min each (in counterbalanced order), (d), then injected the observers with LiCl, and (e) finally (after the observers had recovered from the acute affects of toxicosis), offered each observer a choice between Diets Cin and Coc for 22 hr (Galef, 1987).

As can be seen in Figure 9, I found that observer rats formed a strong aversion to whichever food their respective demonstrators had not eaten and, during the 22-hr test period, ate only the food their demonstrators had eaten (Galef, 1986b; see also Galef et al., 1990). Similar influences of demonstrators on the diet preferences of observers were found even when a delay of 8 days was imposed between the interaction of demonstrator and observer and direct diet sampling and experience of illness by observers (Galef, 1987).

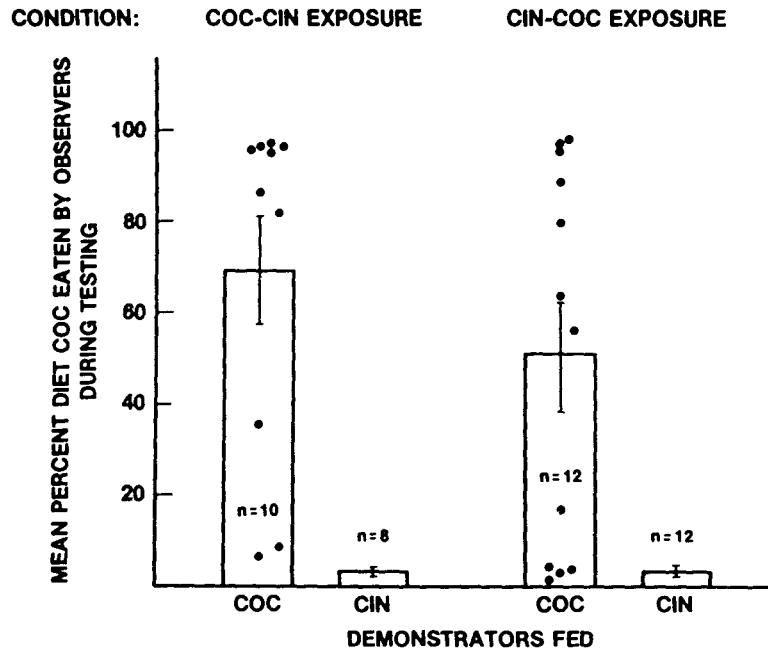


Figure 9. Mean amount of Diet Coc eaten by observers during testing as a function of the diet fed to their demonstrators and the order in which observers ate Diet Cin and Diet Coc before injection with lithium chloride solution (Galef, 1986b).

Learning where to look for food. Galef et al. (1987) found that rats in a maze will spontaneously follow trained conspecific leaders through the maze. They also found that rats trained to follow conspecifics through a maze will follow potential leaders that have eaten a "safe" food with significantly higher probability than they will follow potential leaders that have eaten an "unsafe" food. Follower rats were trained for 8 trials/day for 26 days to enter the same goal box as their respective leaders. Each follower was then offered a sample of a palatable diet (Diet NPT) and poisoned. Subsequently, followers entered the same goal box as leaders fed the "dangerous" Diet NPT on only 58 percent of trials and entered the same goal box as leaders fed the "safe" diet on which the followers were maintained on 90 percent of trials.

Analysis of the Chemical Stimulus

As mentioned at the conclusion of the overview of our earlier work presented at the beginning of the present chapter, our early findings (Galef and Stein, 1985) indicated that substances carried on the breath of demonstrator rats

might provide the contextual cues that render diet-identifying cues effective in altering the diet preferences of observer rats.

Norway rats are a good species in which to differentiate general species-characteristic substances from substances specific to breath. Rats breathe only through their noses, not through their mouths. Hence, if substances providing an effective context for enhancing diet preference are carried on rat breath, comparison of the chemical constituents of air removed from the noses of rats with the chemical constituents of air removed from the mouths of rats should permit identification of relevant compounds.

Figure 10 shows a typical reconstructed ion chromatogram generated by analysis of sulfur compounds in air taken from the noses of rats, as well as the points at which carbonyl sulfide (COS) and carbon disulfide (CS₂) elute.

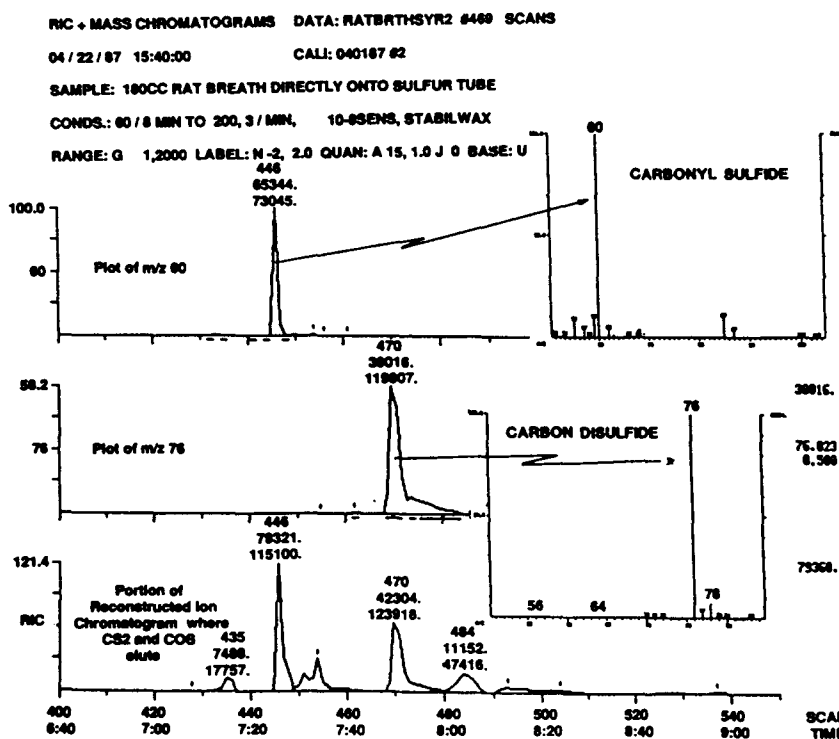


Figure 10. Reconstructed ion chromatograms of rat breath showing molecular ions for COS and CS₂. The spectrum of CS₂ consists mainly of the molecular ion m/z 76, the sulfur-containing isotope ion at m/z 78 as well as a small fragment ion at m/z 64. The spectrum of COS consists primarily of its molecular ion at m/z 60, and an isotope ion at m/z 62 (Galef et al., 1988).

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No sulfur compounds were detected in any air samples taken from the mouths of rats and both COS and CS₂ (but no other sulfur volatiles) were detected in all air samples taken from the noses of rats (Galef et al., 1988).

Of course, finding COS and CS₂ in air taken from the noses of rats, but not in air taken from their mouths, does not provide evidence that either compound plays a role in social influence on diet selection. As described in detail in Galef (1986a; see also Galef et al., 1985; Galef and Stein, 1985), we have found that those Norway rats exposed to foods dusted onto the head of an anesthetized conspecific, but not those rats exposed to the same foods dusted onto a rat-sized, cotton surrogate, subsequently exhibit an enhanced preference for the food with which their "demonstrator" was dusted. If we were to find that CS₂ acts, as does presence of a conspecific, to provide a context within which exposure to a food enhances subsequent preference for that food, such evidence would be consistent with the view that CS₂, which we have found in rat breath, plays a role in normal social transmission of diet preference.

We allowed naive, food-deprived rats to interact for 1/2 hr with either: (a) an anesthetized demonstrator rat that had eaten either Diet Cin or Diet Coc (Anes-Dem groups), (b) a cotton-batting surrogate rat rolled in either Diet Cin or Diet Coc and then moistened with six drops of CS₂ at a concentration of 1 ppm in distilled water (Surr + CS₂ groups), or (c) a cotton-batting surrogate rat rolled in either Diet Cin or Diet Coc and moistened with six drops of distilled water (Surr groups). Each subject next ate, first Diet Coc and then Diet Cin, each for 15 min, was then injected with LiCl, and finally chose for 22 hr between Diet Cin and Diet Coc. As can be seen in Figure 11, only the diet choices of subjects in Anes-Dem and Surr + CS₂ groups were affected by diet exposure. Both CS₂ and a demonstrator rat served as a context that permitted exposure to food odors to effect later food choice (Galef et al., 1988).

Practical Applications

There is an obvious use for any substance that, like CS₂, might augment the attractiveness of foods to rats or to mice. By adding that attractive substance to a poison bait, one might increase ingestion of the bait and, thus, increase its efficacy in rodent control.

There is evidence that placing an aqueous solution of CS₂ near a food substantially increases intake of that food, relative to control samples of food without CS₂. For example, over six nights, free-living, wild Norway rats in a pig barn, livestock feeding pen and pheasant holding pen all ate more than three times as much from baiting stations containing a CS₂ solution (at a concentration of 10 ppm) as from unscented baiting stations (Mason et al., 1989).

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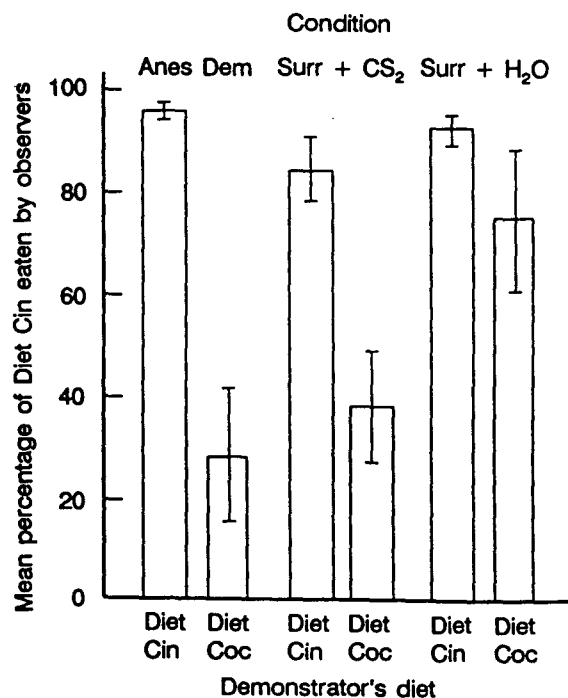


Figure 11. Mean percent Diet Cin eaten by observers during testing (Galef et al., 1988).

In the laboratory, domesticated mice ate significantly more of samples of food moistened with dilute CS₂ solutions than of samples of the same food moistened with distilled water (Bean et al., 1988), and domesticated rats ate less of a plain bait than of the same bait mixed with 50 ppm starch Xanthate, a substance which slowly releases CS₂ (N.J. Bean, personal communication, May 29, 1990). Although preliminary, these data are consistent with the view that dilute solutions of CS₂ may enhance intake of poison baits by murid rodents and, thus, may be useful in control of rodent pests (Galef and Mason, 1989).

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