# *Social Learning*

## *Psychological and Biological Perspectives*

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# *Communication of Information Concerning Distant Diets in a Social, Central-Place Foraging Species:* Rattus norvegicus[1]

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In environments characterized by an unpredictable and patchy distribution of foods, social birds or mammals that forage from a central site (e.g., a burrow, roost, or nesting site) can benefit from exchange of information with conspecifics about the availability and distribution of foods (Bertram, 1978; DeGroot, 1980; Erwin, 1977; Waltz, 1982; Ward & Zahavi, 1973). Relatively unsuccessful foragers able to extract relevant information from their more successful fellows could learn both the identity of foods successful foragers are exploiting and the locations of those foods. Such socially-acquired information could enhance the foraging efficiency of relatively unsuccessful individuals.

Wild Norway rats are social, central-place foragers; in natural circumstances, each rat lives as a member of a colony inhabiting a fixed system of burrows; when foraging, colony members disperse from their burrow, feed, and then return to it (Calhoun, 1962; Telle, 1966). Thus, Norway rats are an ecologically appropriate choice for laboratory experiments examining ways in which social interaction might facilitate food acquisition in a social, central-place foraging species.

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[1] An article similar to the present one has been published, under the title "Olfactory communication among rats: Information concerning distant diets," in D. Duvall (Ed.), *Chemical signals in vertebrates IV: Ecological, evolutionary and comparative aspects of vertebrate chemical signalling.* (1986). New York: Plenum.

## THE LABORATORY PARADIGM

The procedures used in the studies described below simulated a natural situation in which a foraging rat ingests a food at some distance from its burrow, returns to its burrow, and then interacts with a burrow-mate. Our initial purpose was to discover whether, as a result of such interaction (1) the burrow-mate could acquire information concerning the food the forager had eaten and (2) whether the burrow-mate would use the information acquired from its fellow when selecting foods for ingestion.

### The Basic Experiment

During the experiments described below, subjects were housed in same-sex pairs in cages divided in half by screen partitions. To simplify exposition, I refer to the "successful forager" in each pair as a *demonstrator* and the other member of that pair as an *observer*.

The basic experiment, schematized in Figure 6.1, was carried out in five steps:

*Step 1.* Demonstrator and observer were maintained together with ad lib access to Purina Laboratory Rodent chow and water for a 2-day period of familiarization with both apparatus and cage-mate.

*Step 2.* The demonstrator was moved to the opposite side of the screen partition from its observer and food-deprived for 24 hr to ensure that the demonstrator ate when given the opportunity to do so.

*Step 3.* Chow was removed from the observer's side of the cage (in preparation for testing) and the demonstrator was moved to a cage in a separate room and allowed to feed for 30 min on either cinnamon-flavored diet (Diet Cin) or cocoa-flavored diet (Diet Coc).

*Step 4.* The demonstrator was returned to the observer's side of the cage and demonstrator and observer were allowed to interact for 15 min.

*Step 5.* The demonstrator was removed from the experiment and the observer was offered a choice between two weighed food cups, one containing cinnamon-flavored diet (Diet Cin) and one containing cocoa-flavored diet (Diet Coc).

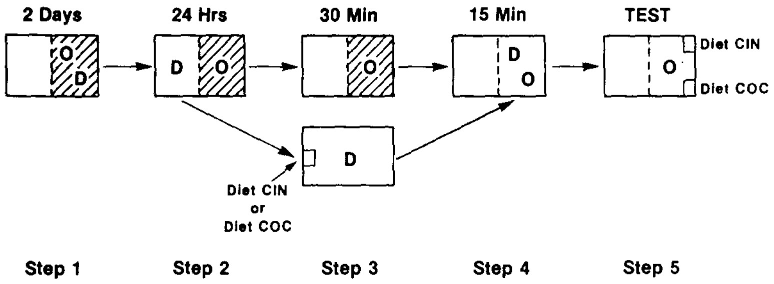

**Figure 6.1.** Schematic diagram of the procedure of the basic experiment. O = observer; D = demonstrator; hatching indicates maintenance diet present in cage. (Galef & Wigmore, 1983. Copyright 1983 by Bailliere Tindall. Reprinted by permission of the publisher and authors.)

Figure 6.2 shows the mean amount of Diet Coc, as a percentage of total amount eaten, ingested during testing (Step 5) by observers whose demonstrators had eaten either Diet Coc or Diet Cin during Step 3 of the experiment. As can be seen in Figure 6.2, (1) those observers whose demonstrators ate Diet Coc ate a far greater percentage of Diet Coc than did those observers whose demonstrators ate Diet Cin, and (2) effects of demonstrators' diet on observers' diet preference were still observable 48–60 hr after interaction of demonstrator and observer. The results of this first experiment clearly show both that an observer rat can extract from a demonstrator information identifying the diet that demonstrator had eaten at a time and place distant from the locus of demonstrator-observer interaction and that this extracted information is sufficient to bias its recipient's subsequent selection of diet.

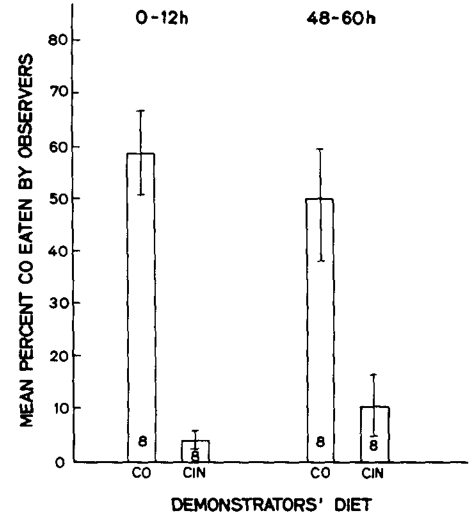

**Figure 6.2.** Mean amount of cocoa-flavored diet ingested, as a percentage of total amount eaten, by observers whose demonstrators ate either cocoa- or cinnamon-flavored diet. CO = cocoa-flavored diet; Cin = Cinnamon-flavored diet. (Galef & Wigmore, 1983. Copyright 1983 by Bailliere Tindall. Reprinted by permission of the publisher and authors.)

## Variations on a Theme

We have repeated the basic experiment described above many times: with a variety of different diets (Galef & Wigmore, 1983), with hungry and replete observers, with male demonstrator-observer pairs and female ones, with wild and domesticated rats, with demonstrator-observer pairs familiar with one another and with pairs that had never met prior to their interaction during Step 4 of the experiment, with both old demonstrators and observers and young ones, and with observers selecting distinctively flavored fluids rather than solids for ingestion (Galef, Kennett, & Wigmore, 1984). In every case, we have seen robust enhancement of observers' preferences for their respective demonstrators' diets. Similarly, Posadas-Andrews and Roper (1983) and Strupp and Levitsky (1984), using rather different paradigms, have repeatedly observed demonstrator influence on subsequent diet selection by observers. The phenomenon of demonstrator influence on observer diet preference seems a general one in Norway rats, not dependent on some restricted set of experimental parameters for its expression.

## Effects of the Passage of Time

In the basic experiment illustrated in Figure 6.1, observers and demonstrators interacted immediately after demonstrators had eaten diets and observers had the opportunity to choose between diets immediately following extraction of information from their respective demonstrators. Free-living rats must expend time in returning from a feeding site to their burrows. In the field, foragers departing from their burrows must expend further time in reaching a feeding site. If the capacity of rats to transmit information concerning a food eaten at a distance from their burrow functions in information exchange in natural settings, communication must occur even if there are delays both between a successful forager's ingestion of a food and its return to its burrow and between the interaction of a successful forager with other rats and the latter's arrival at a potential feeding site. In terms of the laboratory analogue illustrated in Figure 6.1, rats must be able to tolerate delays between Steps 3 and 4 and between Steps 4 and 5 and still successfully exchange information.

Figures 6.3a and 6.3b show the results of experiments in which independent groups of subjects experienced varying delays (1) between a demonstrator feeding and its interaction with an observer and (2) between an observer interacting with a demonstrator and its choosing between diets.

As can be seen in Figure 6.3a, for at least 4 hr after feeding on a diet, demonstrators continued to emit cues sufficient to permit observers to identify their respective demonstrators' diets (Galef & Kennett, 1985). Data presented in Figure 6.3b indicate that observers can use diet-identifying information obtained from demonstrators for 12 to 24 hr after receiving it (Galef, 1983). Both the time course of emission of diet-identifying cues by demonstrators and observer retention of diet-identifying information obtained from demonstrators seem appropriate to permit use of the information transmission system under investigation in natural environments.

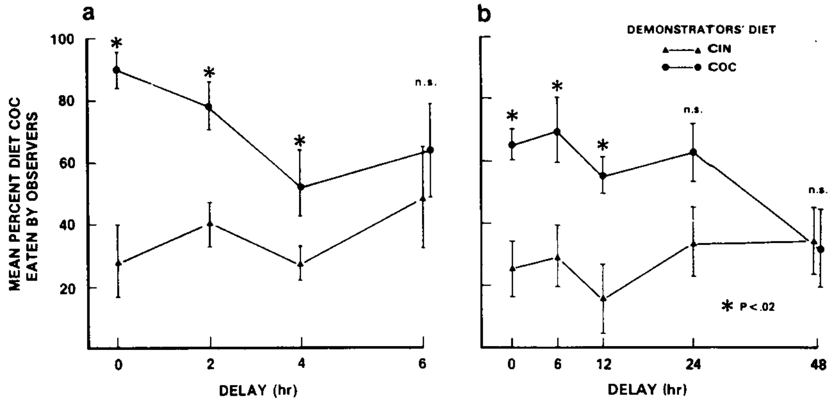

Figure 6.3. Mean amount of cocoa-flavored diet ingested, as a percentage of total amount eaten, by observers whose demonstrators ate Diet Cin or Diet Coc: (3a) as a function of time between ingestion by demonstrator and interaction with observer, (3b) as a function of time between interaction of demonstrator and observer and initiation of testing. (Galef & Wigmore, 1983. Copyright 1983 by Bailliere Tindall. Reprinted by permission of the publisher and authors.)

## Handling of Multiple Messages

Although there is relatively little information available concerning social life in free-living wild rat colonies, it seems reasonable to suppose that each colony member, prior to departing from its colony's burrow system on a foraging expedition, might have the opportunity to acquire information from several conspecifics about foods they had recently ingested. It is, thus, possible that an individual rat, remaining in its burrow and interacting with a succession of colony-mates returning from successful foraging trips, could collect information concerning the entire range of foods returning foragers had exploited.

If rats in their burrows are to make use of information received from a succession of returning colony-mates, they must be able to distinctively encode and store information extracted from each informant. The results of several studies indicate that rats have such a capacity (Galef, 1983). Our method was similar to that outlined in Figure 6.1. However, in the present experiment, each observer, instead of interacting during Step 4 with a single observer that had eaten either Diet Cin or Coc, interacted (in counterbalanced order) for 15 min with each of a series of four demonstrators, one of which had eaten vinegar-flavored diet (Diet Vin), one a coffee-flavored diet (Diet Cof), one a casein and cornstarch-based died (Diet NPT), and one *either* Diet Coc *or* Diet Cin. During testing of observers (Step 5 of Figure 6.1), each observer was offered a choice between Diets Cin and Coc. As can be seen in the left-hand panel of Figure 6.4, those observers one of whose four demonstrators had eaten Diet Coc preferred Diet Coc, whereas those observers one of whose four demonstrators had eaten Diet Cin preferred that diet. Of course, it might have been that the two diets selected for testing (Diets Cin and Coc) were simply the most salient of those offered to demonstrators. To control for this possibility, the entire experiment was repeated using Diets Cin, Coc, and NPT as irrelevant diets and Diets Cof and Vin as critical test items. As can be seen in the right-hand panel of Figure 6.4, those observers one of whose four demonstrators ingested Diet Cof preferred Diet Cof, whereas those observers one of whose four demonstrators ingested Diet Vin preferred Diet Vin. These findings are consistent with the hypothesis that a rat remaining in its burrow and interacting with a succession of returning successful foragers is able to construct an inventory of foods currently available in the larger environment and exploited by its fellows.

## Transmission of Aversions to Distant Diets

Naive rats could benefit not only from information acquired from conspecifics concerning diets those conspecifics have eaten, but also from information about toxic diets more knowledgeable individuals have learned to avoid. We therefore undertook experiments simulating situations in which a rat departs from its burrow, ingests a novel, toxic food, returns to its burrow, and while suffering toxicosis interacts with a burrow-mate. We then presented the burrow-mate with a choice between the novel food its demonstrator had been trained to avoid and a second novel food (Galef, Wigmore, & Kennett, 1983).

Our experimental method was similar to that employed in the basic experiment (see Figure 6.1) except that each demonstrator, after eating either Diet Cin or Diet Coc for 30 min (Step 3 of Figure 6.1), was injected intraperitoneally with 1% of body weight of either 2% (w/vol) LiCl or saline solution. Demonstrators then interacted with observers for either 30 min or 2 hr (Step 4 of Figure 6.1). As can be seen in Figure 6.5, observers exhibited a marked preference for their respective demonstrators' diets even if demonstrators were suffering toxicosis during the period that observers interacted with them.

Analysis of the causes of failure of transfer of aversion indicated that although (1) the diet-identifying cues emitted by a demonstrator are adequate conditional stimuli for taste aversion learning (observers, themselves poisoned after interacting with demonstrators fed either Diet Cin or Diet Coc, developed aversions to their respective demonstrators' diets, Galef et al., 1983) and (2)

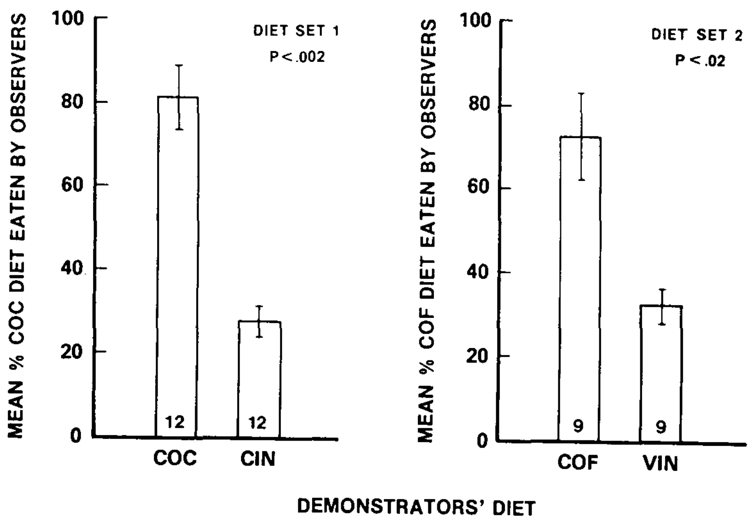

Figure 6.4. Mean percent Diet Coc (left-hand panel) or Diet Cof (right-hand panel) eaten by observers one of whose demonstrators ingested, respectively, either Diet Cin or Coc, or either Diet Cof or Vin. (Galef, 1983. Copyright 1983 by the American Psychological Association. Reprinted by permission of the author and publisher.)

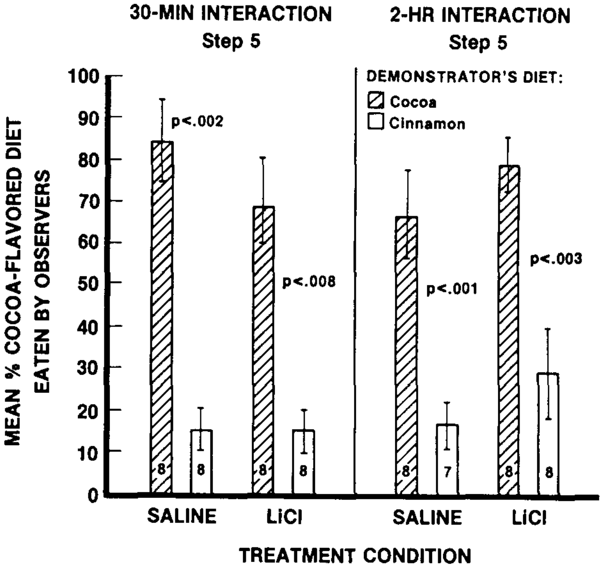

Figure 6.5. Mean amount of cocoa-flavored diet, as a percentage of total amount eaten, ingested by observers whose demonstrators ate either cocoa-flavored or cinnamon-flavored diet and were then injected with LiCl solution or saline. (Galef, Wigmore, & Kennett, 1984. Copyright 1984 by the American Psychological Association. Reprinted by permission of the authors and publisher.)

demonstrators emit cues adequate to serve as unconditional stimuli in a taste-aversion learning paradigm (Bond, 1982; Lavin, Freise, & Coombes, 1980), observers do not, at least under the conditions we employed, associate CS and UCS. Rats seem to transmit information about what foods to eat more readily than information about what foods to avoid (Galef, 1985; for an interesting exception see Gemberling, 1984).

## USE OF EXTRACTED INFORMATION IN ORIENTATION OF FORAGING

Although the experiments described above indicate that a successful forager can provide information about diets it has ingested far from the locus of information transfer, these studies do not provide evidence that such information can be used by its recipients to facilitate their later foraging. To investigate the usefulness of socially transmitted information in increasing foraging efficiency, we introduced our subjects into the environment depicted in overhead schematic in Figure 6.6. The rule here was that each of three discriminable foods was available at a different, fixed location: cheese-flavored diet (CH Diet) in the central arm of the maze, cocoa-flavored diet (CO Diet) in the right arm, and cinnamon-flavored diet (CIN Diet) in the left. Only one of the three diets was accessible to a subject on any given day, and the particular diet available to a subject on any day was randomly selected.

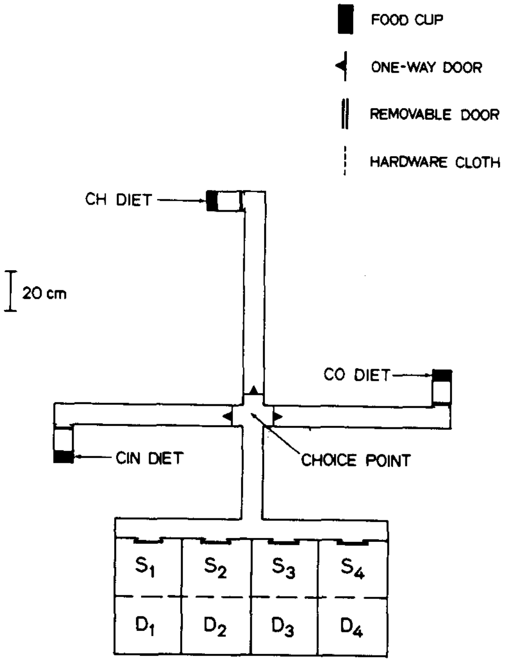

**Figure 6.6.** Plan view of apparatus. Ch = cheese-flavored diet; Cin = Cinnamon-flavored diet; Co = cocoa-flavored diet; S = subject; D = demonstrator. (Galef & Wigmore, 1983. Copyright 1983 by Bailliere Tindall. Reprinted by permission of the publisher and authors.)

Each subject ($S_n$ in Figure 6.6) was given four trials/day using a correction procedure. On the first trial of each day, each subject had no information as to which food was available, and therefore had only one chance in three of selecting the correct arm of the maze. If it chose the correct arm, it could eat for a few minutes. If it didn't, it was locked in the arm it had chosen for a few minutes and the first trial was repeated until the subject found the food. Trials 2, 3, and 4 of each day were run in the same fashion.

Each subject could, in effect, tell the experimenter when it understood this little world by exhibiting more or less perfect performance in its first choices on Trials 2, 3, and 4 of each day. Once a given subject had reached the necessary criterion of performance on Trials 2, 3, and 4, testing was instituted.

On each test day, for 15 min prior to Trial 1 of that day, each subject was allowed to interact with a demonstrator rat ($D_n$ in Figure 6.6) that had eaten the diet that was going to be available to that subject on that day. That is, if cheese-flavored diet was going to be available to $S_3$ on a given day, $S_3$'s demonstrator, $D_3$, was fed cheese-flavored diet for 30 min and then allowed to interact with $S_3$ for 15 min prior to initiating Trial 1 of testing of $S_3$.

To determine whether subjects were capable of using information acquired from demonstrators to enhance foraging efficiency, we compared the probability of a correct response on the first choice of the first trial of each day of testing (when information from a demonstrator was available to subjects) with the probability of a correct response on the first choice of the first trial of each of the last days of training (when no information from a demonstrator was available to subjects). As can be seen in the left-hand panel of Figure 6.7, 4 of our 7 subjects were able to use the information provided by their respective demonstrators to facilitate location of unpredictable foods (Galef & Wigmore, 1983).

As indicated in a preceding section, rats can distinctively encode diet-identifying information extracted from a series of conspecifics. We have also found that they can use such diet-identifying information, embedded in a series of like messages, to orient foraging trips. In another experiment (Galef, 1983), during testing, instead of allowing each subject to interact with a single demonstrator predicting the food to be available on a given day, we had each subject interact with 4 demonstrators; 3 had eaten irrelevant foods (Diets NPT, Vin, and Cof) and one had eaten the food to be available to the subject on that day. As can be seen in the right-hand panel of Figure 6.7, subjects were still able to extract and use the relevant information in selecting an arm of the maze for initial exploration on test days.

In more recent experiments we have found (Galef, Mischinger, & Malenfant, 1987) that rats trained to follow conspecifics to food in a multi-armed maze will follow a leader that has recently eaten a desirable food with higher proba-

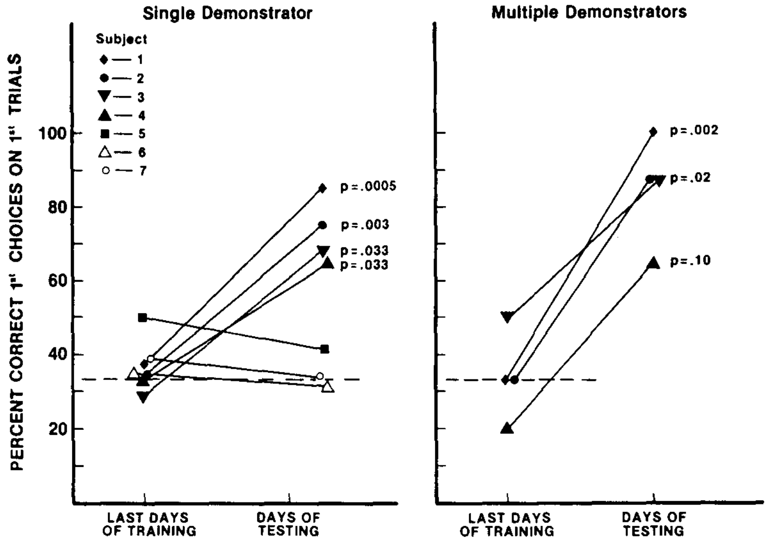

**Figure 6.7.** Percentage of correct first choices on first trials by subjects at the end of training and during testing in the apparatus illustrated in Figure 6.5. (Galef, 1983; Galef & Wigmore, 1983. Copyright 1983 by Bailliere Tindall and the American Psychological Association. Reprinted by permission of the authors and publishers.)

bility than they will follow a leader that has recently eaten an undesirable food. Nine of 10 followers that had been trained to avoid ingesting a novel, highly palatable diet (by feeding them the novel diet and then poisoning them) were less likely to follow leaders that had eaten the averted diet than to follow leaders that had eaten the followers' normal maintenance diet.

These data suggest that a rat in its burrow, interacting with a number of successful foragers, could choose among them and follow those exploiting the most desirable food. The ability to identify the diet eaten by a conspecific, together with a spontaneous tendency to follow others on foraging expeditions (Galef, Mischinger, & Malenfant, 1987) could result, in natural circumstances, in communication of information as to the locations where valuable foods are to be found.

## THE NATURE OF MESSAGES PASSING FROM DEMONSTRATORS TO OBSERVERS

### Implication of Olfactory Signals

An obvious question arising from the experiments described above concerns the means by which an observer rat acquires information from a demonstrator as to the diet that demonstrator has been eating. We have developed several converging lines of evidence, each consistent with the hypothesis that olfactory cues passing from demonstrator to observer are sufficient to allow observer identification of demonstrators' diets.

In order to examine the mode of communication of diet-identifying information from demonstrator to observer, it was necessary to gain some control over their interaction. We employed a procedure similar to that depicted in Figure 6.1, but with one important modification. During the period of demonstrator-observer interaction (Step 4 of Figure 6.1), the members of each demonstrator-observer pair were on opposite sides of the screen partition dividing their cage.

As can be seen in Figure 6.8, observers had no trouble in developing a preference for their respective demonstrators' diets when separated from their demonstrators by a screen during interaction. However, as can also be seen in Figure 6.8, if the screen partition was replaced by a clear Plexiglas partition, demonstrator influence on observer diet preference was completely abolished (Galef & Wigmore, 1983).

Further, we have conducted an experiment in which each demonstrator,

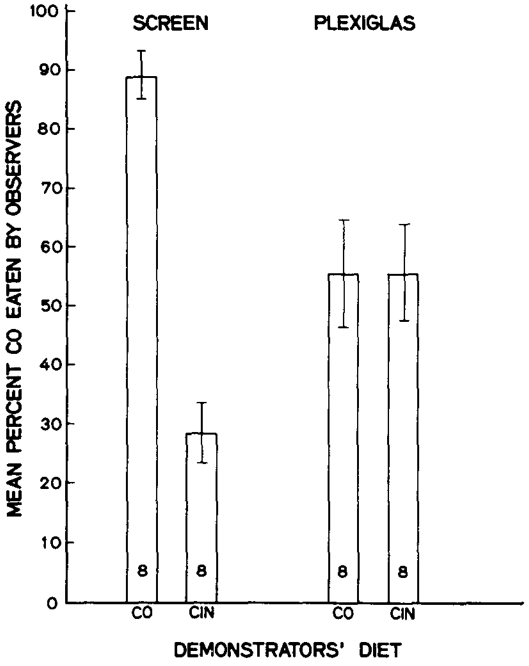

**Figure 6.8.** Mean amount of cocoa-flavored diet ingested, as a percentage of total amount eaten, by observers whose demonstrators ate cinnamon- or cocoa-flavored diet. Left-hand bars, observer and demonstrator separated by a screen partition during interaction. Right-hand bars, observer and demonstrator separated by a Plexiglas partition during interaction. (Galef & Wigmore, 1983. Copyright 1983 by Bailliere Tindall. Reprinted by permission of the publisher and authors.)

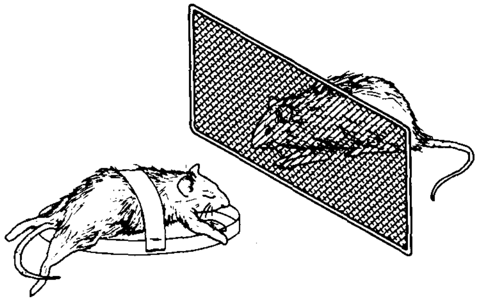

**Figure 6.9.** Illustration of procedure during interaction of anesthetized demonstrator and observer.

after eating either Diet Cin or Diet Coc, was anesthetized and placed 2 in. from and facing a screen partition, with its observer on the other side of the screen (see Figure 6.9). During subsequent preference testing, observers still exhibited (Figure 6.10) a robust preference for their respective demonstrators' diets (Galef & Wigmore, 1983). Also, as one would expect if olfactory cues play an important role in information transfer between demonstrator and observer, observers rendered anosmic by passing zinc-sulfate solution through their nares (Alberts & Galef, 1971) failed to exhibit a preference for their respective demonstrators' diets. Control rats whose nasal passages had been rinsed with saline solution continued to exhibit a preference for their respective demonstrators' diets (See Figure 6.11).

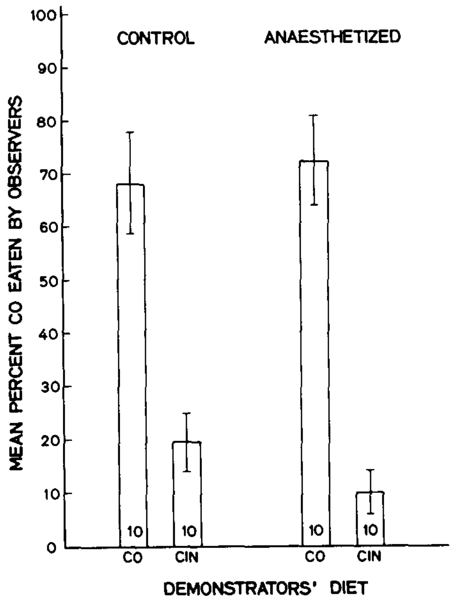

**Figure 6.10.** Mean amount of Diet Coc eaten by observers, as a percentage of total amount ingested. Left-hand bars, observers interacting with intact demonstrators. Right-hand bars, observers interacting with anesthetized demonstrators, as depicted in Figure 6.9. (Galef & Wigmore, 1983. Copyright 1983 by Bailliere Tindall. Reprinted by permission of the publisher and authors.)

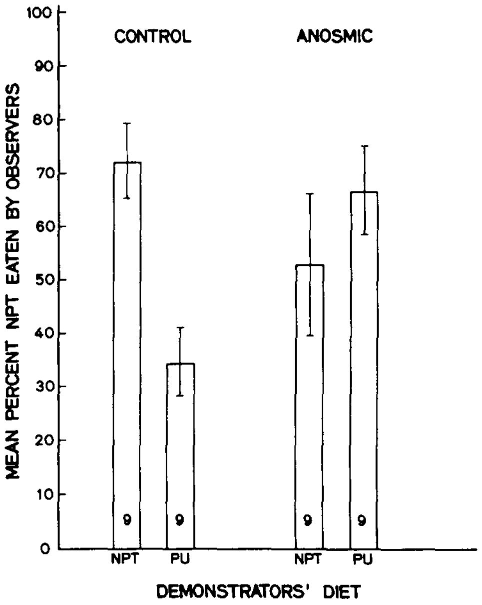

**Figure 6.11.** Mean amount of Diet NPT ingested, as a percentage of total amount eaten, by observers whose demonstrators ate either Diet NPT or Pu. Left-hand bars, observers' nasal cavities rinsed with saline. Right-hand bars, observers' nasal cavities rinsed with $ZnSO_4$, i.e. anosmic. (Galef & Wigmore, 1983. Copyright 1983 by Bailliere Tindall. Reprinted by permission of the publisher and authors.)

Last, but not least, humans, as well as rats, can use olfactory cues emitted by a previously fed rat to tell what diet that rat has been eating. A human observer presented with a dozen rats in random sequence, half having eaten Diet Coc and half Diet Cin, could, by sniffing their breaths, tell with better than 85% accuracy which rat had eaten which diet (Galef & Wigmore, 1983).

## CAUSES OF DEMONSTRATOR INFLUENCE ON OBSERVER DIET PREFERENCE

The simplest behavioral explanation of the observed influence of demonstrators on observers' subsequent diet selection would be something like the following. Rats are always somewhat hesitant to ingest unfamiliar foods (Barnett, 1958; Galef, 1970). As the result of interacting with a demonstrator that has eaten a Diet X and therefore smells of Diet X, an observer rat has been exposed to cues associated with Diet X and should be somewhat familiar with that diet. Therefore, an observer rat that has interacted with a Diet-X-fed demonstrator should eat Diet X in preference to other roughly equipalatable, but totally unfamiliar, diets.

We have conducted a number of experiments designed to test the adequacy of explanations of demonstrator influence on observer diet preference in terms of demonstrator-induced diet familiarity of the sort described above (Galef, Kennett, & Stein, 1985). In every case, the results of our studies have been contrary to the most straightforward predictions from the familiarity hypothesis.

For example, if reduced diet novelty, resulting from observer exposure to diet-identifying cues during interaction with a demonstrator, were responsible for subsequent demonstrator influence on observer diet preference, one would expect observers choosing between two familiar diets to be relatively immune to demonstrator influence on their diet selection. Any additional familiarity with one test diet, resulting from a brief period of interaction with a demonstrator fed that diet, should be overwhelmed by observers' extensive previous experience with both test diets.

We conducted an experiment much like that outlined in Figure 6.1 except that during the 2-day period of familiarization (Step 1 of Figure 6.1), observers in a Cin/Coc pre-exposure group were left alone in their cages and allowed ad lib access to two food bowls, one containing Diet Cin and one containing Diet Coc. Following 2 days of feeding on both Diets Cin and Coc, each observer was exposed for 15 min to an unfamiliar demonstrator that had eaten either Diet Coc or Diet Cin (Step 4 of Figure 6.1). Each observer was then tested for its preference between Diets Coc and Cin (Step 5 of Figure 6.1). Observers in the control group were treated identically to those in the Cin/Coc pre-exposure group except that during familiarization (Step 1 of Figure 6.1), observers in the control group had access to two food bowls containing a powdered form of their standard maintenance diet.

The main results of the experiment are presented in Figure 6.12, which shows the mean amount of Diet Coc, as a percentage of total amount eaten, ingested by observers in Cin/Coc pre-exposure and control groups. As can be seen in the figure, the diet eaten by demonstrators profoundly affected the food choice of observers in both groups. This finding renders unlikely interpretation of the effects of demonstrator influence on observer diet preference as resulting solely from familiarity with the taste or smell of a diet experienced during 15 min of interaction with a demonstrator. Further, simply feeding a rat either Diet Cin or Coc for 15 min (or, for that matter, for 24 hr) prior to offering it a choice between Diets Cin and Coc had no effect on subjects' subsequent choice of diet (Galef et al., 1985).

In the face of such data, it is difficult to maintain the hypothesis that demonstrator influence on observer diet preference is the result of a simple increase in observers' familiarity with their respective demonstrators' diets. An obvious alternative is that the presence of a demonstrator is necessary if experience of diet-identifying cues is to alter observers' subsequent diet preference. It is this hypothesis that has been the guiding principle in our recent research.

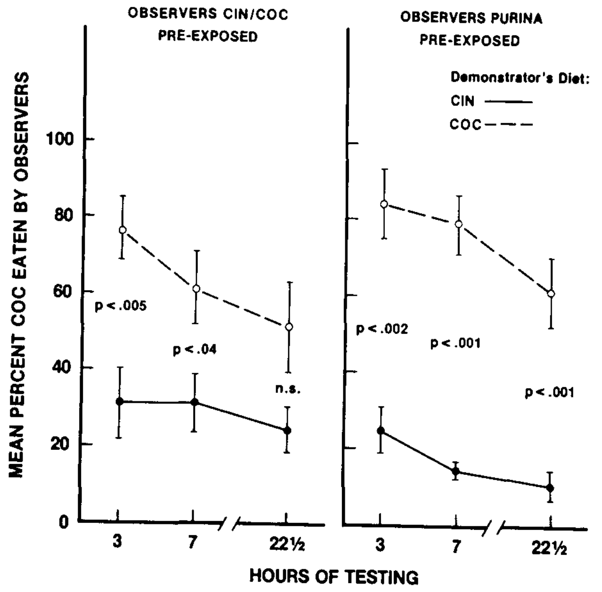

Figure 6.12. Mean amount of Diet Coc ingested by observers either pre-exposed or not pre-exposed to Diets Cin and Coc and whose demonstrators ate either Diets Cin or Coc. (Galef, Kennett & Stein, 1985. Copyright 1985 by the Psychonomic Society, Inc. Reprinted by permission of the authors and publishers.)

## Analysis of Olfactory Cues

Assume, for the sake of argument, that I am correct in asserting that demonstrators do not alter their observers' subsequent diet preference by simply making diet-identifying cues available to observers, rather that demonstrators provide important contextual cues, as well as diet-identifying cues, necessary for demonstrator influence on observer diet preference. If so, then analysis of the message passing from demonstrator to observer presents two separable problems: (1) determination of the source of the diet-identifying cues emitted by demonstrators and (2) determination of the source and nature of the contextual cues, also emitted by demonstrators, that act in concert with the diet-identifying cues to alter observers' subsequent diet preference.

*Diet Identifying Cues.* In order to look more closely at the cues involved in demonstrator influence on observer diet preference, we again changed our experimental procedures slightly. The new procedure was similar to that described in Figure 6.1, but differed both in the way in which demonstrators were made to emit diet-identifying cues (Step 3) and in the treatment of demonstrators and observers during the period of their interaction (Step 4). Rather than feed all demonstrators during Step 3 of the procedure, we employed a variety of techniques for attaching diet-identifying cues to demonstrators. Some demonstrators were allowed to eat Diet Cin or Diet Coc for 30 min, as was done in the basic experiment. Other demonstrators were anesthetized and their faces dusted with either Diet Cin or Diet Coc. Yet other demonstrators were anesthetized and tube-fed one of two distinctively flavored fluids. Some observers, instead of interacting with a demonstrator during Step 4 of the procedure, spent 30 min interacting with a surrogate rat (constructed of cotton-batting and surgical gauze) one end of which had been dusted with either Diet Cin or Coc. Further, instead of permitting demonstrator and observer to interact freely during Step 4, each anesthetized demonstrator was placed in the screen tube of the apparatus illustrated in Figure 6.13. Observers were introduced into the bucket-shaped area of the enclosure, left there for 30 min, then moved back to their respective home-cages for testing (Step 5 of Figure 6.1).

As can be seen in Figure 6.14, 30-min observer interaction with a surrogate demonstrator, dusted with either Diet Coc or Diet Cin, failed to affect observer diet preference during testing (Step 5), providing further evidence of the inadequacy of simple exposure to a diet to produce alterations in observer diet preference. In contrast, exposure to a fed demonstrator, an anesthetized demonstrator powdered with diet, or an anesthetized demonstrator tube-fed a flavored solution each had the capacity to alter observers' diet selection during testing.

The finding that diet applied to the faces of demonstrators enhanced diet preference in their observers indicates that ingestion of a diet by a demonstrator is not critical in demonstrator production of diet-identifying cues. The finding that demonstrators stomach-loaded with a flavored solution also induced observers to increase their preference for the solution placed in the stomach of demonstrators indicates that particles of food clinging to the fur and vibrissae of demonstrators are not necessary for transmission of diet-identifying information to observers. Taken together the results of the present study (Galef et al., 1985; Galef & Stein, 1985) show that both particles of food on the exterior of rats and portions of diet in the stomach of rats provide cues sufficient to permit observers to identify their respective demonstrators' diets.

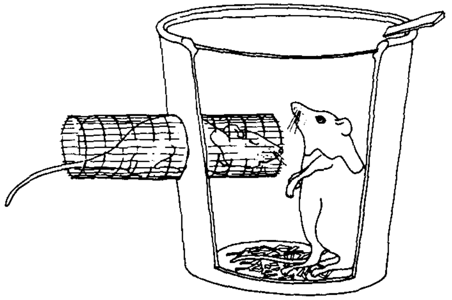

Figure 6.13. Illustration of apparatus used to analyze diet-identifying and contextual cues. (Galef & Stein, 1985. Copyright 1985 by the Psychonomic Society, Inc. Reprinted by permission of the authors and publisher.)

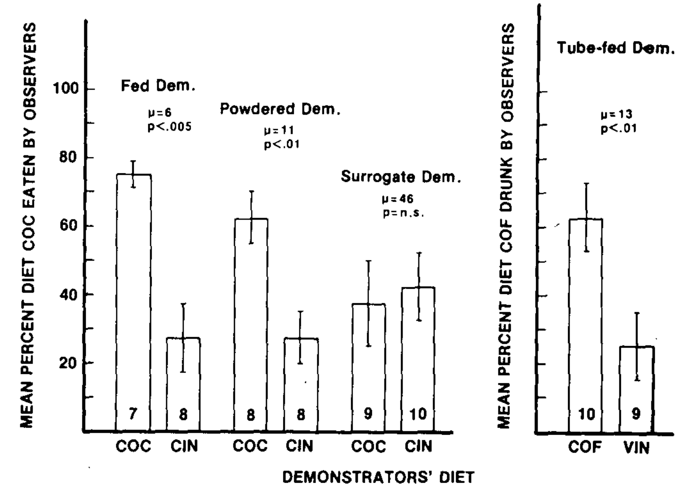

Figure 6.14. Left-hand panel: Mean amount of cocoa-flavored diet eaten, as a percentage of total amount ingested, by observers interacting with demonstrators or surrogates. Right-hand panel: Mean amount of coffee-flavored solution, as a percentage of total amount drunk, ingested by observers whose demonstrators were tube-fed with either coffee- or vinegar-flavored solution.

*Contextual Cues.* The results of the studies presented in Figure 6.14 also suggest that a demonstrator rat provides a context within which exposure to diet-identifying cues alters observers' subsequent diet preference. Observer preference was not affected by exposure to a diet presented on a surrogate, but was affected by exposure to the same diet presented on the face of a rat. Further, the procedure employed in these studies provides an opportunity to define more precisely the nature of the contextual cues which, in combination with diet-identifying cues, produce demonstrator influence on observer diet preference.

We allowed observers to interact for 30 min in the apparatus illustrated in Figure 6.13 with demonstrators treated in one of four ways: (1) Observers in the powdered-face group interacted with anesthetized demonstrators whose faces had been rolled in either Diet Cin or Diet Coc. (2) Observers in the dead-powdered-face group interacted with demonstrators that had been sacrificed by anesthetic overdose and had their faces rolled in either Diet Cin or Diet Coc prior to the demonstrators' introduction into the apparatus. (3) Observers in the powdered-rear group interacted with anesthetized demonstrators whose rear ends were rolled in Diet Cin or Diet Coc. These demonstrators were introduced into the screen tube of the apparatus illustrated in Figure 6.13 with their rear ends inside the bucket and their heads outside of it. Last, (4) observers in the surrogate group were allowed to interact in the apparatus with a rat-size cotton-batting stuffed length of tubular gauze one end of which had been rolled in either Diet Cin or Diet Coc.

Figure 6.15 presents a measure of the degree of influence of the various sorts of demonstrators on their respective observers' subsequent diet preferences during testing (Step 5 of Figure 6.1). The summary descriptive statistic, cocoa-demonstrator/cinnamon-demonstrator ratio, was calculated by dividing the mean percentage of Diet Coc eaten during testing by observers whose demonstrators had been coated with Diet Coc by the mean percentage Diet Coc eaten during testing by observers whose demonstrators had been coated with Diet Cin. Each histogram in the figure summarizes data from 16–20 observers, half of which interacted with demonstrators coated with Diet Coc and half with demonstrators coated with Diet Cin. The greater the Cocoa-demonstrator/Cinnamon-demonstrator ratio the greater the influence of demonstrators' diets on observers' subsequent diet preference.

To summarize the results of a series of statistical analyses discussed in detail elsewhere (Galef & Stein, 1985): (1) Observers in powdered-face groups consistently exhibited a significant tendency to choose for ingestion the diets applied to their respective demonstrators. (2) Observers in surrogate groups exhibited no tendency to select the same diet for ingestion that their respective demonstrators had been fed. (3) Observers in dead-powdered-face and powdered-rear groups were both significantly less affected in their diet selection by demonstrators than were observers in powdered-face groups, and significantly more affected by demonstrators than were observers in surrogate groups. Taken together these findings suggest (1) that simple exposure of an observer rat to the smell of a diet is not sufficient to enhance observer preference for that diet, and (2) that the contextual cues emitted by demonstrator rats, producing preference for a diet in their observers, are both widely distributed and most concentrated at the anterior end of live rats. These findings do not, of course, satisfactorily resolve the issue of the nature or origins of the effective contextual cues emitted by demonstrator rats. Determination of the active chemicals involved in potentiating observer preference for demonstrators' diets must await biochemical analyses. We will attempt such analyses in the future, but I suspect that identification of the critical agent or agents will prove as difficult in the present case as it has in other attempts to chemically define mammalian pheromones.

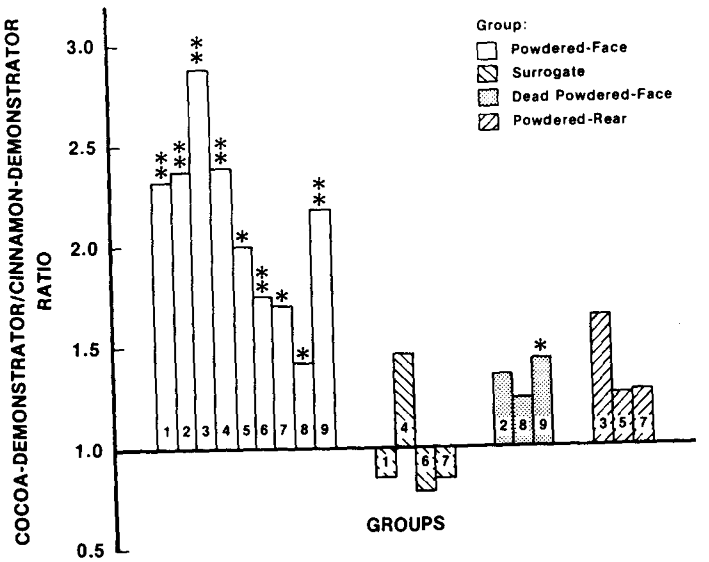

Figure 6.15. Cocoa-demonstrator/Cinnamon-demonstrator ratios of groups of observers interacting with demonstrators and surrogates in the apparatus illustrated in Figure 6.13. Observers were randomly assigned across groups labeled with the same integer. * = $p < .05$, ** = $p < .01$. (Galef & Stein, 1985. Copyright 1985 by the Psychonomic Society, Inc. Reprinted by permission of the authors and publisher.)

## SUMMARY AND CONCLUSIONS

The series of studies described above provide compelling evidence that naive rats have the capacity to extract information from recently fed conspecifics, permitting identification of the food conspecific individuals have eaten. Recipients of such information are biased in their subsequent food selection by diet-related cues they experience during interaction with a fed individual. Recipients of diet-identifying information, acquired during social interaction, can use that information to orient their subsequent foraging activities.

Information concerning distant diets is contained in olfactory signals passing from recently fed rats to naive ones. These olfactory cues both permit recipient identification of the diet eaten by a conspecific and provide an as yet undefined social context that results in subsequent enhanced preference for diets eaten by informants.

Norway rats, like honeybees, the only other species of social, central-place foragers whose sharing of information concerning distant diets has been examined in detail (Gould, 1976; von Frisch, 1967; Wenner, 1971), possess a number of behavioral mechanisms for the social enhancement of foraging efficiency (See Galef, 1977, 1983, 1984a, for reviews). The convergent evolution of social learning mechanisms in species as phyletically diverse as bees and rats suggests that laboratory study of social effects on feeding in other social, central-place foragers should prove fruitful.

Social learning provides a relatively little understood alternative to individual learning for the development of adaptive feeding repertoires. Social, central-place foraging species, both vertebrate and invertebrate, offer as yet unexplored opportunities for increased understanding of the mechanisms of social learning and the development of diet choice.

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