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Responses of Observer Rats (*Rattus norvegicus*) to Complex, Diet-Related Signals Emitted by Demonstrator Rats

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We explored the effects of complex, food-identifying signals emitted by demonstrator Long-Evans rats (*Rattus norvegicus*) on food preferences of their observers. In Experiments 1 and 2, observers identified each of 2 or 3 foods their demonstrators had eaten before interacting with observers. In Experiment 3, individual observers interacted with groups of demonstrators. Some of these demonstrators had eaten one food, some another. Observers then chose between the two foods. The greater the proportion of demonstrators in a group that had eaten a diet, the greater the proportion of that diet the observers ate. In Experiment 4, each observer interacted over several weeks with a series of demonstrators and preferred each of the foods its demonstrators had eaten. In sum, the food preferences of observers were affected by several different types of complex, food-identifying signals like those one might expect rats to encounter outside the laboratory.

After interacting with a recently fed demonstrator rat, a naive observer rat will exhibit an enhanced preference for the food that its demonstrator ate (Galef & Wigmore, 1983; Posadas-Andrews & Roper, 1983). In the laboratory such social influences on diet selection are large and long lasting (Galef, 1989; for reviews see Galef, 1986a, 1988; Galef, Kennett, & Wigmore, 1984). Furthermore, socially acquired information about the foods that others are eating can facilitate identification of both nutritionally adequate (Beck & Galef, 1989) and toxic diets in laboratory settings (Galef, 1986b, 1987; for review see Galef & Beck, in press). Consequently, it has seemed reasonable to suggest that social influence may play a significant role in the development of adaptive patterns of food choice by free-living, wild Norway rats as it does in laboratory-maintained, domesticated rats (Galef & Beck, in press).

In almost all previous studies of social influences on diet choice in rats, both those carried out in our laboratory (see Galef, 1988, for review) and those completed elsewhere (Heyes & Durlach, 1990; Posadas-Andrews & Roper, 1983; Strupp & Levitsky, 1984), observer rats interacted with conspecific demonstrators that had relatively simple histories of recent food intake: (a) Each demonstrator with which an observer rat interacted ate only a single food during the 24-hr period before its contact with an observer, and (b) any observer that interacted with more than one demonstrator interacted with demonstrators that had all eaten the same food during the 24 hr immediately before the interaction (for an exception see Galef, 1983).

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It is reasonable to suppose that in the world outside the laboratory, (a) individual, free-living Norway rats often eat several different foods before they return to their burrows and interact with colony mates; (b) at any given time, not all members of a rat colony are eating the same food; and (c) over a period of days or weeks, an individual rat may interact with many others, each of which has been eating a different food. Thus, in natural circumstances a rat is likely to receive an extended series of complex food-related messages as the result of interacting with its fellows. If so, situations previously studied in the laboratory have involved overly simplified food-related communications relative to those that rats probably experience in natural habitat. Consequently, the validity of extrapolations from previous laboratory studies of social effects on food choice to field situations is open to question.

In this series of experiments, we explored the effects of various sorts of complex, food-related signals emitted by demonstrator rats on the later food preferences of their respective observers. In Experiments 1 and 2, we examined the effects on observers' later food choices of interacting with demonstrators that had eaten either two (Experiment 1) or three (Experiment 2) different foods immediately before they interacted with their respective observers. In Experiment 3, we determined the effects on individual observers' later food choices of simultaneous interaction with several demonstrators, some that had eaten one food and some that had eaten another. Finally, in Experiment 4, we looked at the effects on observers' food choices of a succession of interactions with individual demonstrators, each of which had eaten a different diet unfamiliar to the observer.

Experiment 1

In this experiment naive observer rats interacted briefly with demonstrator rats, each of which had eaten two different foods immediately before it interacted with its observer. We wanted to know whether naive observers would extract usable diet-identifying information from the complex olfactory signals emitted by such demonstrators.

Method

Subjects

One hundred forty-four, 42-day-old, female, Long-Evans rats (*Rattus norvegicus*), born in the McMaster University vivarium and weaned at 21 days of age, served as observers. Observers were maintained in groups of 3 or 4 same-sex littermates on ad lib Purina Rodent Laboratory Chow #5001 pellets and water until they were 41 days of age. At that time we randomly assigned each of these 144 observers to one of two studies that differed in the food to be offered to observers during testing (see Step 5 of *Procedure*). Within each of these two studies, observers were again assigned randomly to one of eight groups that differed in the foods to be fed to demonstrators immediately before each demonstrator interacted with its observer (see Steps 2 and 3 of *Procedure*). An additional 144, 49- to 56-day-old, female rats from the same source as observers served as demonstrators. These demonstrators had served as observers in other experiments.

Apparatus

Throughout the 4 days of the experiment, each observer was housed individually in a 24 cm wide × 19 cm high × 18 cm deep, wire mesh hanging cage. Each demonstrator was maintained alone in a 19 × 16.5 × 30.5 cm wire mesh hanging cage in a room separate from that housing the observers, except during the 30-min period of interaction between a demonstrator and its observer (see Step 4 of *Procedure*), when each demonstrator was introduced into its observer's cage.

Foods

The four foods used in this experiment were prepared by mixing powdered Purina Rodent Laboratory Chow #5001 with, respectively, 1% by weight McCormick's Fancy Ground Cinnamon (Diet Cin), 2% by weight Hershey's Pure Cocoa (Diet Coc), 1% by weight bulk ground anise (Diet Ani), or 2% by weight bulk ground marjoram (Diet Mar).

Experimental Design

Each of the two studies that constituted the experiment was a 2 × 2 × 2 design in which diets eaten by demonstrators were the independent variables. During Steps 2 and 3 of the Procedure, each demonstrator ate one diet from the pair Diet Cin–Diet Coc (Factor 1) and one diet from the pair Diet Mar–Diet Ani (Factor 2). The order in which demonstrators ate the diet selected from each pair was the third factor. As mentioned earlier, Study 1 and Study 2 differed in the pair of diets (either Diet Cin–Diet Coc or Diet Ani–Diet Mar) between which each observer chose during testing (Step 5 of *Procedure*).

Procedure

The experiment was carried out in five steps.

Step 1. Demonstrators were placed on a 23-hr food-deprivation schedule and offered powdered Purina Rodent Laboratory Chow #5001 for 1 hr/day for 2 consecutive days.

Step 2. After a third 23-hr period of food deprivation, each demonstrator was offered for 15 min a weighed food bowl containing a flavored food.

Step 3. Immediately after removal of the first food bowl from each demonstrator's cage, each demonstrator was offered for 15 min a second weighed food bowl containing a different flavored food than that available during Step 2.

Demonstrators were each fed one of eight sequences of diets during Steps 2 and 3. If a demonstrator that received Diet Coc in Step 2 and Diet Ani in Step 3 is designated as having received treatment Coc–Ani, then demonstrators received the following eight treatments during Steps 2 and 3: Cin–Ani, Cin–Mar, Coc–Ani, Coc–Mar, Ani–Cin, Mar–Cin, Ani–Coc, and Mar–Coc.

Step 4. Immediately after the completion of Step 3, each demonstrator was placed in the cage of an observer and left to interact with that observer for 30 min.

Step 5. At the end of the 30-min period of demonstrator–observer interaction, the demonstrator was removed from the observer's cage, and the observer was offered for 23 hr a pair of weighed food bowls. Seventy-two observers were offered a choice between Diets Mar and Ani (Study 1), and 72 observers were offered a choice between Diets Cin and Coc (Study 2).

The experimenter replaced any spillage in the appropriate bowl and determined the amount of each diet eaten by each demonstrator during Steps 2 and 3 and by each observer during Step 5.

Data Analysis

To examine the effects of the interaction with a demonstrator on the food preferences of observers, we determined the percentage of each observer's total intake during the 23-hr choice test (Step 5) that was either Diet Ani (for those observers in Study 1, which were offered a choice between Diets Ani and Mar) or Diet Cin (for those observers in Study 2, which were offered a choice between Diets Cin and Coc). We then calculated a group mean and standard error from these individual percentage scores. The individual percentage scores were arcsine transformed before use in the analyses of variance.

Results

The main results of Experiment 1 are presented in the top and bottom panels of Figure 1, which shows, respectively, the mean amount of Diet Ani eaten by observers in Study 1, as a percentage of the total amount of food each observer ate during Step 5, and the mean amount of Diet Cin eaten by observers in Study 2, as a percentage of the total amount of food each observer ate during Step 5.

As can be seen in the top panel of Figure 1, those observers whose demonstrators had eaten Diet Ani ate significantly more Diet Ani when offered a choice between Diets Ani and Mar than did those observers whose demonstrators had eaten Diet Mar, $F(1, 71) = 25.94$, $p < .00001$. Furthermore, neither of the two other independent variables nor any of the first- or second-order interactions between variables significantly affected observers' preferences between Diets Mar and Ani, all $Fs(1, 71) < 0.42$, all *ps*, *ns*. The effects of demonstrators on the food preferences of the 72 observers in Study 1 are easily described; those observers that interacted with demonstrators fed Diet Ani ate a greater percentage of Diet Ani during testing than did those observers that interacted with demonstrators fed Diet Mar.

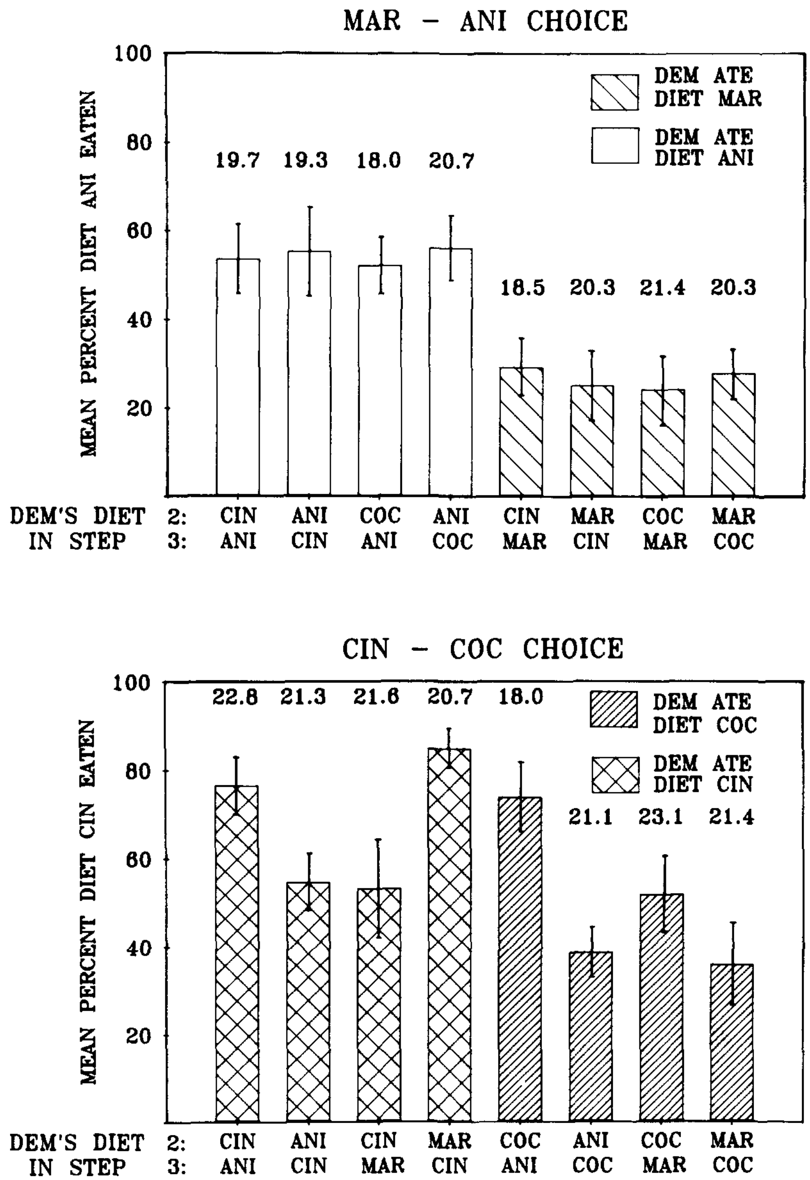

Figure 1. Mean percentage of Diet Ani and Diet Cin eaten by observers during testing in Experiment 1. (Top panel is data from Study 1; bottom panel is data from Study 2. Lines indicate *SE*, and numbers above the bars indicate the g of diet eaten by observers in a given group during testing. MAR = marjoram diet; ANI = anise diet; CIN = cinnamon diet; COC = cocoa diet, and DEM = demonstrator.)

As can be seen in the bottom panel of Figure 1, the food choices of observers in Study 2 that chose between Diets Cin and Coc during testing were more complexly determined than were the food choices of observers in Study 1 that chose between Diets Ani and Mar. Although the 36 observers in Study 2 that interacted with demonstrators fed Diet Cin ate a significantly greater percentage of Diet Cin than did the 36 observers in Study 2 that interacted with demonstrators fed Diet Coc, $F(1, 71) = 13.22$, $p < .0009$, there was also a significant effect on observers' diet choices of order of diet presentation to demonstrators. In this study, when demonstrators ate one of the diet pair Ani–Mar after eating one of the diet pair Cin–Coc, their observers did not exhibit any effect of demonstrator's diet on their preference for Diet Cin during testing (Newman-Keul's test, *ns*); to the contrary, when demonstrators ate one of the diet pair Ani–Mar before eating one of the diet pair Cin–Coc, the observers exhibited a robust effect of the demonstrator's diet on their preference for Diet Cin (Newman-Keul's test, $p < .01$). As one might expect, the interaction between the effects of Factor 1 and Factor 3 on observer preference for Diet Cin during testing was significant, $F(1, 71) = 5.63$, $p < .03$. Thus, in Study 2, the order in which demonstrators ate diets had an effect on the diet choices of observers. No similar effect was found in Study 1.

Demonstrators ate an average of 2.8 ± 0.1 g during Step 2 and an average of 2.4 ± 0.1 g during Step 3.

Discussion

The results of Experiment 1 indicate that naive rats can sometimes extract diet-identifying information from recently fed demonstrators, even if the diet-identifying cues emitted by those demonstrators are complex. Effects of interaction with demonstrators on the later food choices of naive observers were influenced by several factors: the particular combination of foods eaten by demonstrators, the order in which those foods were eaten, and the food choices presented to observers. Hence, the occurrence of social influences on diet choice is more variable in complex than in simple feeding environments. Still, a naive rat could be expected to extract some usable information from the complex olfactory messages provided by a conspecific that had recently eaten two different foods.

Experiment 2

Experiment 2 was a repetition of Experiment 1, but each demonstrator was fed three rather than two different foods in succession before interacting with an observer.

Method

Subjects

Seventy-two, 42-day-old, female, Long-Evans rats served as observers, and an additional 72, 49- to 56-day-old females served as demonstrators.

Apparatus and Foods

The apparatus and foods used in this experiment were the same as those used in Experiment 1.

Experimental design

The experiment was conducted as two studies, each a 2 × 2 design in which the foods eaten by demonstrators were the independent variables. The two studies differed in the choice of foods given to observers during testing.

Each demonstrator ate three foods, either the pair of Diets Cin and Coc and one diet from the pair Ani–Mar or the pair of Diets Ani and Mar and one diet from the pair Cin–Coc (Factor 1). The order of presentation for the diets of each pair was the second factor.

Procedure

The procedure of the present experiment was identical to that of Experiment 1 except during Steps 2 and 3 when the demonstrators were fed. In the present experiment each demonstrator was offered three weighed food bowls in succession for 10 min each rather than two weighed food bowls in succession for 15 min each.

If a demonstrator that received first a weighed food bowl with Diet Coc, then one with Diet Ani, and last one with Diet Cin is designated as a member of Group Coc–Ani–Cin, then the eight groups examined in the present experiment can be described as: Cin–Ani–Coc, Coc–Ani–Cin, Cin–Mar–Coc, Coc–Mar–Cin, Ani–Coc–Mar, Mar–Coc–Ani, Ani–Cin–Mar, Mar–Cin–Ani. Those observers that interacted with demonstrators assigned to the first four listed groups (Study 1) were offered a choice between Diets Ani and Mar during testing; those observers interacting with demonstrators in the last four groups (Study 2) were offered a choice between Diets Cin and Coc during testing. Note that for each group of observers, the second of the three diets fed to their respective demonstrators was one of the two diets presented during testing. Consequently, the results of this experiment describe the effects on observers' diet choices only of the second of a series of three diets eaten by their respective demonstrators.

Results

The main results of Experiment 2 are presented in the left and right panels of Figure 2, which show, respectively, the mean amount of Diet Ani eaten by observers in Study 1, as a percentage of the total amount of food each ate during testing and the mean amount of Diet Cin eaten by observers in Study 2, as a percentage of the total amount of food each ate during testing.

As can be seen in the left panel of Figure 2, those observers in Study 1 whose demonstrators had eaten Diet Ani ate significantly more Diet Ani during the 23-hr choice test between Diets Ani and Mar than did those observers whose demonstrators ate Diet Mar, $F(1, 35) = 9.26$, $p < .005$. Neither the effect of order of presentation of Diets Cin and Coc nor the first-order interaction between variables was significant, both $Fs(1, 35) < 2.36$, both *ps*, *ns*.

Similarly, as can be seen in the right panel of Figure 2, those observers in Study 2 whose demonstrators had eaten Diet Cin ate significantly more Diet Cin during the 23-hr choice between Diets Cin and Coc than did those observers whose demonstrators ate Diet Coc, $F(1, 35) = 13.94$, $p < .001$. Again neither the effect of order of presentation of Diets Mar and Ani nor the first-order interaction between the variables was significant, both $Fs(1, 35) < 0.61$, both *ps*, *ns*.

Demonstrators ate an average of 2.1 ± 0.4 g of the first diet they were offered, 1.7 ± 0.3 g of the second, and 1.6 ± 0.4 g of the third.

Discussion

The results of the present experiment extend those of Experiment 1. Food choices of observers can be influenced by complex olfactory messages provided by demonstrators that have eaten three and perhaps even more different foods shortly before interacting with observers.

Given the finding in Study 2 of Experiment 1 that demonstrators that ate either Diet Mar or Diet Ani after eating Diet Cin or Diet Coc did not influence their respective observers' later preferences for Diet Cin, it is surprising that observers in Study 2 of the present experiment (observers whose demonstrators also ate Diet Mar or Ani after eating Diet Cin or Coc) were influenced in their preference for Diet Cin by the diets eaten by their respective demonstrators. Either the absolute amount of Diet Mar or Ani eaten by demonstrators after eating Diet Cin or Coc is important in determining whether observers can detect Diet Cin or Coc on their demonstrators or one of our two experiments produced an anomalous result. The anomaly, if present, is not particu-

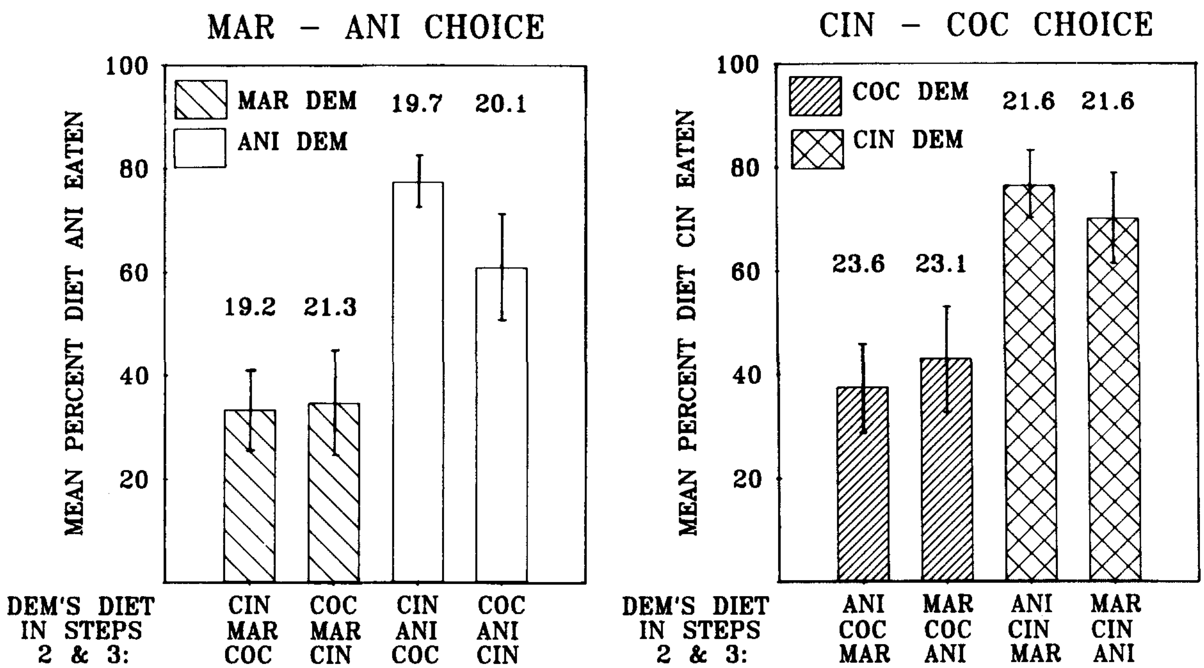

Figure 2. Mean percentage of Diet Ani and Diet Cin eaten by observers during testing in Experiment 2. (Left panel is data from Study 1; right panel is data from Study 2. Lines indicate *SE*, and numbers above the bars indicate the g of diet eaten by observers in a given group during testing. MAR = marjoram diet; ANI = anise diet; CIN = cinnamon diet; COC = cocoa diet, and DEM = demonstrator.)

larly important because, regardless of the outcome of the present experiments in which only four diets were used, it seems intuitively very likely that there exist both diets the odor of which can mask the odor of other diets and diets the odor of which does not mask the odor of other diets. If so, the outcome of experiments such as these will depend in large measure on the choice of diets fed to demonstrators. The most that studies such as Experiments 1 and 2 can establish is an ability of observers sometimes to extract usable diet-identifying information from demonstrators that have eaten several different foods. Positive findings establish such an ability; negative ones simply suggest limits on its usefulness.

Experiment 3

A free-living Norway rat, sharing a burrow system with others of its species, is likely to encounter not only individual conspecifics that have eaten several different foods (Experiments 1 and 2) but also many different individuals, some of which have been eating one food and some of which have been eating another.

The results of previous studies of social transmission of diet preference do not provide much insight into the effects of encountering several rats, some of which have eaten one diet and some of which have eaten a second diet, on an observer's later choice between the two diets. It is, for example, possible that after interacting with several demonstrators, some that ate the first diet and some that ate the second diet, an observer will show no effect of its social interactions on its later choice between the two diets; the different messages received from different demonstrators may simply negate one another. If so, the range of circumstances outside the laboratory in which social interactions can affect diet choice is appreciably reduced.

Method

Subjects

One hundred eighty, 42-day-old, male, Long-Evans rats from the McMaster University vivarium served as observers in this experiment. An additional 224, forty-nine-day-old, male, Long-Evans rats served as demonstrators.

Apparatus

The demonstrators were maintained in groups of either 3 or 4 unrelated animals in 20 × 15 × 38 cm, plastic, shoe-box cages and were fed individually in 19 × 16.5 × 30.5 cm, wire mesh hanging cages. The observers were housed and tested individually in 19 × 16.5 × 30.5 cm, stainless steel hanging cages.

Procedure

The experiment was carried out in four steps.

Step 1. The demonstrators were assigned randomly to one of nine conditions (five conditions with 4 demonstrators in a group and four conditions with 3 demonstrators in a group). Each group of demonstrators was housed together in a shoe-box cage and placed on a 23-hr food-deprivation schedule for 2 consecutive days. On each day each demonstrator was removed from its group cage to an individual cage where it was offered a food cup that contained powdered Purina Rodent Laboratory Chow #5001 for 1 hr/day.

Step 2. After a third 23-hr period of food deprivation, each demonstrator was returned to its individual feeding cage and offered a weighed food bowl with either Diet Mar or Diet Ani (see *Method* of Experiment 1 for diet composition) for 1 hr. The nine groups of demonstrators differed in the percentage of each group's members fed Diet Mar or Diet Ani. If a group of 4 demonstrators in which 3 members were fed Diet Ani and 1 was fed Diet Mar is designated as Group 3-Ani–1-Mar, then the following nine groups of either 3 or 4 demonstrators were used in the present experiment: 0-Ani–4-Mar, 1-Ani–3-Mar, 2-Ani–2-Mar, 3-Ani–1-Mar, 4-Ani–0-Mar, 0-Ani–3-Mar, 1-Ani–2-Mar, 2-Ani–1-Mar, and 3-Ani–0-Mar.

Step 3. After eating for 1 hr, each demonstrator was returned to its group cage, and a naive observer was added to each group for 1 hr. As soon as the 1st observer was removed from a group's cage, it was replaced with a 2nd observer that was also permitted to interact with that group for 1 hr. Some groups of demonstrators were food deprived for a fourth 23-hr period, and Steps 2 and 3 were repeated. In all such cases, the proportion of demonstrators in a group fed Diet Ani was changed between days so that particular groups of demonstrators did not participate repeatedly in the same condition.

Step 4. Immediately after the 1-hr interaction between observer and demonstrators, each observer was returned to its home cage and for 23 hr was offered a choice between two weighed food cups, one with Diet Mar and the other with Diet Ani.

At the end of each observer's 23-hr period of testing, the experimenter determined the amount of each of the two diets eaten by each observer.

Results

The main results of Experiment 3 are presented in Figure 3, which shows the mean amount of Diet Ani eaten by observers in each of the nine groups, as a percentage of the total amount of food that they ate during testing.

As can be seen in Figure 3, the percentage of Diet Ani eaten by observers during testing was affected by the proportion of

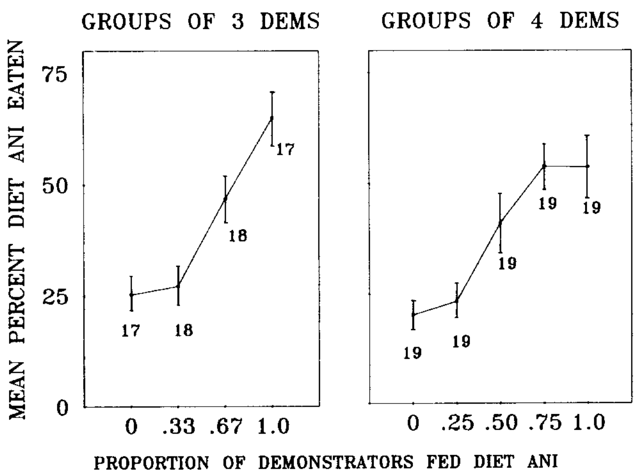

Figure 3. Mean percentage of Diet Ani eaten by observers during testing in Experiment 3 as a function of the proportions of a group's demonstrators fed Diet Ani. (Vertical lines indicate *SE*, and numbers given below the data points indicate the sample size of each observer group. DIET ANI = anise diet, and DEMS = demonstrators.)

their demonstrators that had eaten Diet Ani during Step 2, $F(1, 4) = 7.91$, $p < .0001$, and $F(1, 3) = 12.80$, $p < .0001$. With respect to the purposes of this experiment, the most interesting comparisons are among those observers that interacted during Step 3 with groups of demonstrators some members of which ate Diet Ani and some Diet Mar (e.g., Groups 1-Ani–3-Mar, 2-Ani–2-Mar, and 3-Ani–1-Mar and Groups 1-Ani–2-Mar and 2-Ani–1-Mar). Comparison of the percentage of Diet Ani eaten during testing by observers in Group 1-Ani–2-Mar and 2-Ani–1-Mar revealed a significant effect of the composition of demonstrator groups on observers' diet choices, $t(34) = 3.72$, $p < .001$. Similarly, comparison of the percent Diet Ani eaten during testing by observers in Groups 1-Ani–3-Mar, 2-Ani–2-Mar, and 3-Ani–1-Mar revealed a sensitivity on the part of observers to the proportion of their demonstrators fed Diets Mar and Ani, $F(1, 2) = 7.45$, $p < .002$; observers in Group 1-Ani–3-Mar ate significantly less Diet Ani during testing than did observers in Group 3-Ani–1-Mar (Newman-Keul's test, $p < .01$).

During Step 4, the mean total amount of diet eaten by observers in the nine treatment conditions ranged from 23.7 ± 1.1 g to 25.5 ± 1.0 g. During Step 3, the mean amount of Diet Mar eaten by demonstrators ranged from 7.8 ± 0.7 g to 9.0 ± 0.4 g and the mean amount of Diet Ani from 7.8 ± 0.4 g to 8.5 ± 0.2 g.

Discussion

It is clear from the results of Experiment 3 that observers are sensitive to the relative number of demonstrators with which they interacted that ate each of two diets; the greater the proportion of a group of demonstrators that ate one of those diets, the greater the preference of their observers for that diet (see also Chou, 1989).

In a discussion of the effects of the frequency of two behavioral variants in a population on the probability that a naive animal will acquire one of the variants by social learning, Boyd and Richerson (1985) described two general types of social learning models: unbiased models and frequency-dependent, biased models. In an unbiased model the probability that a naive individual will acquire one of two behavioral variants by social learning is equal to the frequency of that variant in the population. Frequency-dependent bias requires that naive individuals be disproportionately likely to acquire the more (or less) common of two behavioral variants present in a population of potential models.

When we initiated this experiment, it was our hope that we could determine whether transmission of food preferences from demonstrators to observers was biased or unbiased in Boyd and Richerson's (1985) sense of the terms, Unfortunately, the effect of demonstrators on the diet preferences of their respective observers in the present experiment was not of sufficient magnitude and the error variance in observers' diet preferences was too great to provide a completely convincing answer. It might be noted that in three of the four instances available for examination (Groups 1-Ani–2-Mar, 2-Ani–1-Mar, 1-Ani–3-Mar, and 3-Ani–1-Mar), observers seemed to show biased transmission (i.e., the food preferences of observers interacting with mixed groups of demonstrators did not differ significantly from those of observers interacting with homogeneous groups of demonstrators). However, the experiment needs to be repeated with a procedure that produces greater between- and less within-groups variance to resolve the issue convincingly.

Experiment 4

In order for information about the foods conspecifics have eaten to play a continuing role in the food choices of rats outside the laboratory, individual rats must be affected by such information on many different occasions. If each rat was only susceptible to one or two social influences, although social learning might be important in the weaning process, it would not play much role in foraging decisions made later in life.

To determine the efficacy of a succession of interactions with demonstrators on the food choices of observers, we exposed individual observer rats to a succession of demonstrators, each recently fed a different food unfamiliar to the observer. After each interaction with a demonstrator, the observers were tested to determine the effects of that interaction on their food preferences.

Method

Subjects

Twenty-four, 42-day-old, female, Long-Evans rats, born in the McMaster University vivarium to breeding stock acquired from Charles River Canada (St. Constant, Quebec) and maintained in the vivarium as described in *Method* of Experiment 1, served as observers. Half the observers were assigned randomly to a control group, half to an experimental group. An additional 216, 49- to 56-day-old female rats that had served as observers in other experiments, served as demonstrators in the present experiment.

Foods

Eight foods were composed by mixing powdered Purina Rodent Laboratory Chow #5001 with, respectively, 1% by weight McCormick's Fancy Ground Cinnamon (Diet Cin), 2% by weight Hershey's Pure Cocoa (Diet Coc), 2% by weight bulk ground marjoram (Diet Mar), 1% by weight bulk ground anise (Diet Ani), 0.4% by weight bulk ground cloves (Diet Clo), 0.5% by weight bulk ground cumin (Diet Cum), 0.5% by weight bulk ground rosemary (Diet Ros), and 0.5% bulk ground cardamon (Diet Car). All bulk herbs and spices were obtained from the Horn of Plenty (Dundas, Ontario, Canada).

Procedure

Observers. On each of the 23 consecutive days of the experiment, each of the 24 observers was offered a choice for 23½ hr/day between Diet Coc and one of the other seven diets. On 9 days (Days 1, 5, 8, 10, 12, 15, 17, 20, and 22 of the experiment) each observer interacted for ½ hr with a single, unfamiliar demonstrator immediately after that demonstrator had eaten for 1 hr. The 12 observers assigned to the control group each interacted with a demonstrator fed unadulterated powdered Purina Rodent Laboratory Chow #5001 on Days 1, 5, 8, 10, 12, 15, 17, 20, and 22. The 12 observers assigned to the experimental group each interacted with a demonstrator fed one of the seven flavored diets on each of the 9 days on which interaction occurred. If the notation Day 1–Diet Cin is read as "on Day 1 of the experiment each observer in the experimental group interacted with a demonstrator fed Diet Cin," then the conditions for the 23 days of the experiment were: Day 1–Diet Cin, Day 5–Diet Mar, Day 8–Diet Ani, Day 10–Diet Clo, Day 12–Diet Cum, Day 15–Diet Ros, Day 17–Diet Car, Day 20–Diet Cin, Day 22–Diet Mar.

For 23½ hr after the interaction between each demonstrator and its observer and for the next 1–3 days (see Figure 4 for details), all 24 observers were offered a choice between Diet Coc and the diet fed to the demonstrators assigned to the experimental group before the demonstrators interacted with their respective observers. For example, as can be seen in Figure 4, (a) on Day 1, each observer in the experimental group interacted for ½ hr with a demonstrator fed Diet Cin, and (b) for 23½ hr on Days 1–4, all observers in both the experimental and control groups were offered a choice between Diets Cin and Coc.

Demonstrators. Each of the 24 demonstrators that interacted with an observer on 1 of the 9 days when interaction between demonstrators and observers occurred had been placed on a feeding schedule 3 days earlier. On each of 2 successive days, each demonstrator was deprived of food for 23 hr and then fed unflavored, powdered Purina Rodent Laboratory Chow #5001 for 1 hr. After a third 23-hr period of food deprivation, each demonstrator was fed the appropriate diet, either flavored powdered Purina Rodent Laboratory Chow #5001 (in the case of those demonstrators that interacted with observers assigned to the experimental group) or unflavored powdered Purina Rodent Laboratory Chow #5001 (in the case of those demonstrators that interacted with observers assigned to the control group), for 1 hr before interacting with an observer.

The experimenter determined both the amount of diet eaten by each demonstrator during the hr before it interacted with its observer and the amount of each diet eaten by each observer during successive 23½-hr periods throughout the 23 days of the experiment. The experimenter then calculated the percentage of each subject's total food intake during each 23½-hr period of food choice that was Diet Coc.

Results

The main results of Experiment 4 are presented in Figure 4, which both illustrates the details of the procedure of Experiment 4 and shows the mean amount of Diet Coc eaten by individual observers in both control and experiment groups, as a percentage of the total food intake of each during daily, 23½-hr periods of food choice. As can be seen in Figure 4, the diets eaten by demonstrators that interacted with observers in the experimental group had a significant effect on the acceptance of each of a series of unfamiliar foods by their observers (Mann-Whitney U tests; see Figure 4 for p values). Although effects of demonstrators on their respective observers' subsequent diet choices were observable for only 1 or 2 days in this experiment, there is reason to believe that minor modifications in experimental procedure can produce far more enduring effects (Galef, 1989).

Also shown in Figure 4 (right ordinate) is the mean total amount of food eaten by observers in control and experimental groups during daily 23½-hr choice tests. As one would expect by chance alone, there was a significant ($p < .05$)

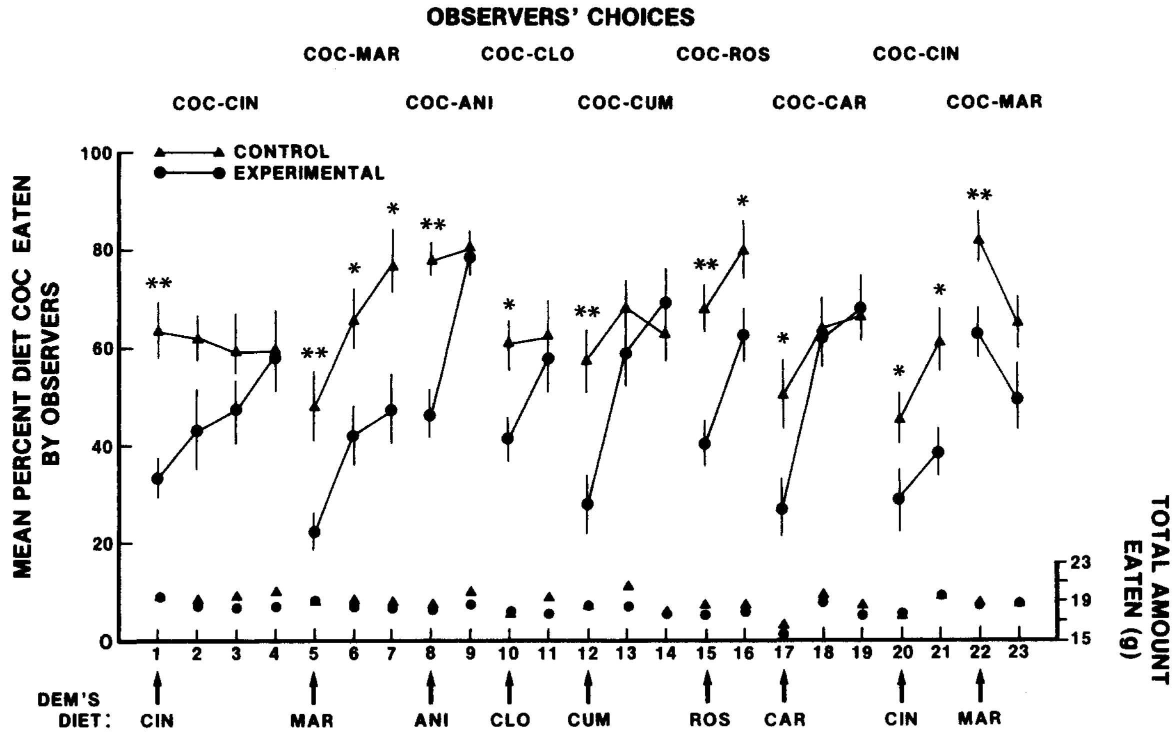

Figure 4. Mean percentage of Diet Coc eaten and total amount eaten by observers in control and experimental groups during daily 23½-hr tests. (Pairs of diets shown at the top of the figure indicate the choice offered to observers on each day. Diets shown at the bottom of the figure indicate foods presented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

difference in the total amount eaten by observers in control and experimental groups on only 1 day (Day 13) of the 23 of the experiment. Demonstrators ate an average of 8.2 ± 0.3 g of chow and 8.5 ± 0.4 g of flavored diet on the 9 days when they interacted with observers.

Discussion

Mainardi (1980) proposed that socially transmitted information can be either conservative or innovative in its effects on behavior. In the former case, for example, in song learning by many passerine birds, the main effect of social information is to maintain a familiar behavior in a population. In the case of innovative social learning, for example, in the spread of milk-bottle opening among British tits (Fisher & Hinde, 1949; Sherry & Galef, 1984), the effect of social learning has been to introduce a novel behavior into a population.

The design of previous studies of social influence on diet selection in rats has emphasized conservative aspects of the phenomenon, the ability of social interaction to bring the food choices of naive weanlings into line with those of their elders. The results of Experiment 4 demonstrate more clearly than those of previous experiments the innovative potential of social influences on diet choice. As individual colony members discover a succession of new foods, they can increase the probability that colony mates will sample each of those new foods.

General Discussion

Numerous laboratory studies have found that a naive observer rat, after interacting with one or several conspecific demonstrators fed a single food, exhibits an enhanced preference for that food. The results of our series of experiments extend these earlier results by showing that naive observers can extract diet-identifying information from complex as well as from simple food-related social signals. A demonstrator that has eaten two or three different foods, a group of demonstrators whose members have eaten different foods, and a series of demonstrators each of which has eaten a different food can all provide usable information to their respective observers. Taken together with the robustness (Galef et al., 1984) of the phenomenon of social transmission of information about distant foods (Galef & Wigmore, 1983; Posadas-Andrews & Roper, 1983) and the durability of social effects on diet preference (Galef, 1989), the finding that rats can extract usable information from complex, food-related, social signals suggests that socially acquired information may play a significant role in the development of adaptive patterns of diet choice by Norway rats outside the laboratory.

References

Beck, M., & Galef, B. G., Jr. (1989). Social influences on the selection of a protein-sufficient diet by Norway rats (*Rattus norvegicus*). *Journal of Comparative Psychology, 103,* 132–139.

Boyd, R., & Richerson, P. J. (1985). *Culture and the evolutionary process.* Chicago: Chicago University Press.
Chou, L.-S. (1989). *Social transmission of food selection by rats,* Rattus *spp.* Unpublished doctoral dissertation, University of California at Davis.
Fisher, J., & Hinde, R. A. (1949). The opening of milk bottles by birds. *British Birds, 42,* 347–357.
Galef, B. G., Jr. (1983). Utilization by Norway rats (*R. norvegicus*) of multiple messages concerning distant foods. *Journal of Comparative Psychology, 97,* 364–371.
Galef, B. G., Jr. (1986a). Olfactory communication among rats of information concerning distant diets. In D. Duvall, D. Müller-Schwarze, & R. M. Silverstein (Eds.), *Chemical signals in vertebrates: Vol. 4. Ecology, evolution, and comparative biology* (pp. 119–140). New York: Plenum Press.
Galef, B. G., Jr. (1986b). Social identification of toxic diets by Norway rats (*Rattus norvegicus*). *Journal of Comparative Psychology, 100,* 331–334.
Galef, B. G., Jr. (1987). Social influences on the identification of toxic foods by Norway rats. *Animal Learning & Behavior, 15,* 327–332.
Galef, B. G., Jr. (1988). Communication of information concerning distant diets in a social, central-place foraging species: *Rattus norvegicus.* In T. R. Zentall & B. G. Galef, Jr. (Eds.), *Social learning: Psychological and biological perspectives* (pp. 3–28). Hillsdale, NJ: Erlbaum.
Galef, B. G., Jr. (1989). Enduring social enhancement of rats' preferences for the palatable and the pignant. *Appetite, 13,* 81–92.
Galef, B. G., Jr., & Beck, M. (in press). Diet selection and poison avoidance by mammals individually and in social groups. In E. M. Stricker (Ed.), *Handbook of behavioral neurobiology: Vol 10. Food and water intake.* New York: Plenum Press.
Galef, B. G., Jr., Kennett, D. J., & Wigmore, S. W. (1984). Transfer of information concerning distant food in rats: A robust phenomenon. *Animal Learning & Behavior, 12,* 292–296.
Galef, B. G., Jr., & Wigmore, S. W. (1983). Transfer of information concerning distant foods: a laboratory investigation of the "information-centre" hypothesis. *Animal Behaviour, 31,* 748–758.
Heyes, C. M., & Durlach, P. J. (1990). Social blockade of taste-aversion learning in Norway rats (*Rattus norvegicus*): Is it a social phenomenon? *Journal of Comparative Psychology, 104,* 82–87.
Mainardi, D. (1980). Tradition and the social transmission of behavior in animals. In G. W. Barlow & J. Silverberg (Eds.), *Sociobiology: Beyond nature/nurture* (pp. 227–255). Boulder, CO: Westview Press.
Posadas-Andrews, A., & Roper, T. J. (1983). Social transmission of food preferences in adult rats. *Animal Behaviour, 31,* 265–271.
Sherry, D. F., & Galef, B. G., Jr. (1984). Cultural transmission without imitation: Milk bottle opening by birds. *Animal Behaviour, 32,* 937–938.
Strupp, B. J., & Levitsky, D. A. (1984). Social transmission of food preferences in adult hooded rats (*Rattus norvegicus*). *Journal of Comparative Psychology, 98,* 257–266.

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