Animal Learning & Behavior
1992, 20 (1), 56-62

Social transmission of information about multiflavored foods

BENNETT G. GALEF, JR., and ELAINE E. WHISKIN
McMaster University, Hamilton, Ontario, Canada

We fed demonstrator rats diets made by adding three, four, or five different flavorants to powdered Purina Rat Chow. We then allowed each of these demonstrator rats to interact with a naive observer rat for 30 min. We found that (1) observers exhibited enhanced preferences for many of the individual flavorants in the multiflavored diets that their respective demonstrators had eaten and (2) the probability of an observer exhibiting enhanced preference for an individual flavorant in its demonstrator's diet decreased as the number of flavorants in that diet increased. In Experiment 2, the individual members of pairs of subjects were each fed one of two different four-flavored diets. The subjects in each pair interacted for 30 min, then each chose between two single-flavored diets. One of these single-flavored diets contained a flavorant in the four-flavored food that a subject had itself eaten; the other single-flavored diet contained a flavorant in the four-flavored diet that a subject's partner had eaten. The subjects showed enhanced preferences for six of eight flavorants in the four-flavored diets that their respective partners had eaten.

Results of experiments conducted in several laboratories have shown that after a naive rat (an observer) interacts with a recently fed conspecific (a demonstrator), the observer exhibits an enhanced preference for whatever food its demonstrator ate (Galef & Wigmore, 1983; Grover et al., 1988; Heyes & Durlach, 1990; Posadas-Andrews & Roper, 1983). We have found recently that (1) information concerning several different foods can be transmitted from one rat to another during a single period of social interaction (Galef, Attenborough, & Whiskin, 1990) and (2) while interacting, rats need not act only as demonstrators or only as observers. Each of a pair of rats can exchange information, acting both as a demonstrator for and as an observer of its partner (Galef, 1991).

The present series of studies was undertaken to further explore the ability of rats that had eaten foods with complex flavors both to acquire diet-identifying information from and to exchange diet-identifying information with their fellows. In Experiment 1, each observer rat interacted with a demonstrator that had eaten a food with three, four, or five different flavorants added to it. In Experiment 2, each member of a pair of rats first ate one of two different four-flavored foods and then interacted with its pair mate. In both experiments, we determined whether the subjects' diet preferences were modified by interaction with a conspecific that had eaten a food with more than one flavorant added to it.

This research was supported by grants from the Natural Sciences and Engineering Research Council of Canada and the McMaster University Research Board to B.G.G., Jr. We thank Mertice Clark for helpful comments on earlier drafts of the manuscript and David Hopkins of Purina Mills Inc. (St. Louis) for sharing with us proprietary information concerning the manufacture of Purina Rodent Laboratory Chow 5001. Requests for reprints should be sent to Dr. B. G. Galef, Jr., Department of Psychology, McMaster University, Hamilton, ON, Canada L8S 4K1.

EXPERIMENT 1

In a previous study of the transmission of complex, diet-identifying information from demonstrator rats to their observers (Galef et al., 1990), we fed individual demonstrator rats either two or three different foods in succession and then permitted naive observer rats to interact with these demonstrators. The observer rats were able to extract from their respective demonstrators information concerning each of the two or three different foods that those demonstrators had eaten.

The procedure of feeding demonstrators several different foods in succession is both imprecise and cumbersome: (1) Demonstrator rats determine for themselves the amount of each of the foods offered to them that they eat, and (2) as the number of foods eaten by demonstrators increases beyond two, examining effects of the order of presentation of foods to demonstrators on the ability of their observers to detect those foods leads to an unmanageable proliferation of groups.

In the present experiment, we overcame these methodological difficulties by feeding each demonstrator a single food containing a mixture of flavorants. We thus both gained control of the relative amounts of flavorants eaten by demonstrators and removed the need to examine the effects of order of presentation of demonstrators' diets on social influence on the diet preferences of observers.

Method

Subjects. One hundred ninety-two 42-day-old, experimentally naive female Long-Evans rats, born in the vivarium of the McMaster University Psychology Department to breeding stock acquired from Charles River Canada (St. Constant, Quebec), served as observers. Each observer was reared in a litter that had been culled to 10 pups 1 to 4 days after birth, and each was weaned at 21 days of age. After weaning, and until the observers were 41 days old, they were maintained in polypropylene shoebox cages (35×30×15 cm) in groups of 3 or 4 same-sex littermates with ad-lib access to pellets of Purina Rodent Laboratory Chow 5001 and water.

When the observers reached 41 days of age, each was assigned to one of three studies that differed in the number of flavorants added to their demonstrators' food. Within each study, the observers were assigned to groups that differed both in the particular flavorants added to foods that their respective demonstrators ate (Step 2 of Procedure) and in the flavorants in the pair of foods that each observer chose during testing (Step 4).

An additional 192 female, 49- to 56-day-old Long-Evans rats that had served as observers in previous experiments served as demonstrators in the present experiment.

Foods. During Step 2 of Procedure, each demonstrator ate a food composed of powdered Purina Rodent Laboratory Chow 5001, to which was added a combination of flavorants selected from the following: McCormick's Fancy Ground Cinnamon (Cin), Hershey's Pure Cocoa (Coc), bulk ground anise (Ani), bulk ground marjoram (Mar), bulk ground thyme (Thy), and bulk ground cumin (Cum).

During testing (Step 4 of Procedure), observers were offered a choice of one of three pairs of foods. If a food composed of powdered Purina Rodent Laboratory Chow 5001, to which 2.0% (by weight) Coc had been added, is described as Diet 2.0 Coc, then the three diet pairs offered to subjects during Step 4 of Procedure can be described as Diet 1.0 Cin and Diet 2.0 Coc, Diet 1.0 Ani and Diet 2.4 Mar, and Diet 0.5 Cum and Diet 0.5 Thy.

Procedure. The experiment was carried out in four steps:

Step 1. Each demonstrator and each observer were housed in separate, wire-mesh hanging cages (24×19×18 cm). The observers continued to eat pellets of Purina Rodent Laboratory Chow 5001 ad lib; the demonstrators were placed on a 23-h food-deprivation schedule and offered powdered Purina Rodent Laboratory Chow 5001 for 1 h/day for 2 consecutive days.

Step 2. After a third 23-h period of food deprivation, each demonstrator was offered, for 1 h, a weighed food bowl containing a multiflavored diet.

Step 3. At the end of Step 2, the pellets of chow were removed from each observer's cage, each demonstrator was placed in the home cage of an observer, and the observer and the demonstrator were left to interact freely for 30 min.

Step 4. At the end of the 30-min period of interaction between demonstrator and observer, each demonstrator was removed from the experiment, and each observer was offered a choice, for 23 h, of one of the three pairs of diets described above.

The experimenter determined both the amount of multiflavored diet eaten by each demonstrator during Step 2 and the amount of each diet eaten by each observer during Step 4.

Study 1, Study 2, and Study 3. The three studies that make up the present experiment differed in the number of flavorants added to powdered Purina Rodent Laboratory Chow 5001 offered to demonstrators during Step 2 and in the pair of diets offered to observers during Step 4.

The 18 groups of subjects in the present experiment make it awkward to describe the treatment of each animal in detail in the text. Instead, we refer the reader to the panels of Figures 1, 2, and 3, in which (1) the flavorants (in grams added to 100 g of Purina chow) fed to each group of demonstrators during Step 2 are indicated below each histogram, (2) the pair of diets offered to each observer during Step 4 is described in the floating title above each pair of histograms, and (3) the number of subjects in each group is indicated by the digits within each histogram. It should be noted that the two groups described in any single panel of Figures 1-3 ate diets that differed in only one flavor.

Study 1 (Figure 1). During Step 2, each demonstrator in Study 1 (n = 44; four groups) ate a diet with three flavorants added to it, and, during Step 4, each observer in Study 1 was offered a choice

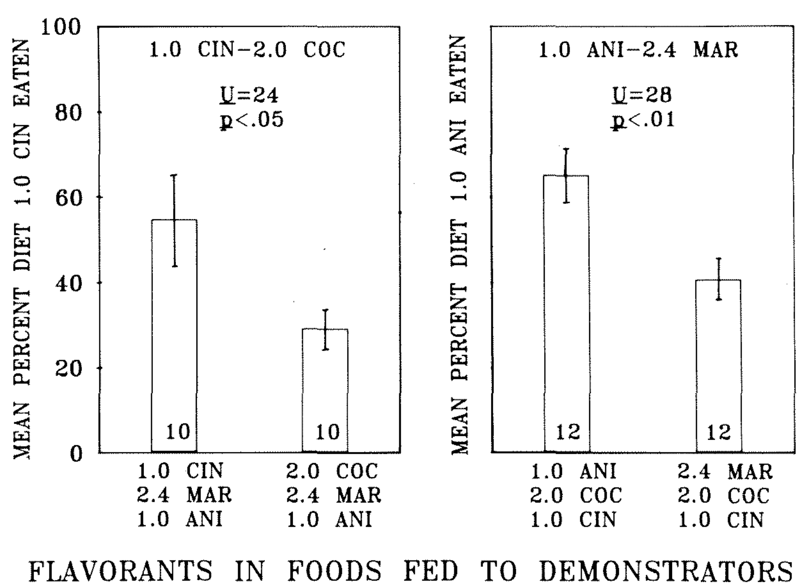

Figure 1. The two panels show the mean amount of Diet 1.0 Cin or Diet 1.0 Ani eaten by observers that had interacted with demonstrators fed three-flavored foods during Step 2 of Procedure (Experiment 1). The choice of diets offered to each group of subjects is indicated by the floating title above each pair of histograms; the flavorants in the foods fed to each group of demonstrators are shown below each histogram. The numbers in each histogram = *n*/group. Flags = ±1 *SEM*.

either between Diet 1.0 Cin and Diet 2.0 Coc or between Diet 1.0 Ani and Diet 2.4 Mar.

Study 2 (Figure 2). During Step 2, each demonstrator in Study 2 (n = 82; eight groups) ate a diet with four flavorants added to it, and, during Step 4, each observer in Study 2 was offered a choice between Diet 1.0 Cin and Diet 2.0 Coc, between Diet 1.0 Ani and Diet 2.4 Mar, or between Diet 0.5 Cum and Diet 0.5 Thy.

Study 3 (Figure 3). During Step 2, each demonstrator in Study 3 (n = 56; six groups) ate a diet with five flavorants added to it, and, during Step 4, each observer in Study 3 was offered a choice between Diet 1.0 Cin and Diet 2.0 Coc, between Diet 1.0 Ani and Diet 2.4 Mar, or between Diet 0.5 Cum and Diet 0.5 Thy.

Results and Discussion

The main results of Experiment 1 are illustrated in Figures 1–3, which present data describing the food choices made during Step 4 of Procedure by observers in Study 1 (Figure 1), Study 2 (Figure 2), and Study 3 (Figure 3) as a function of the flavors in the multiflavored diets fed

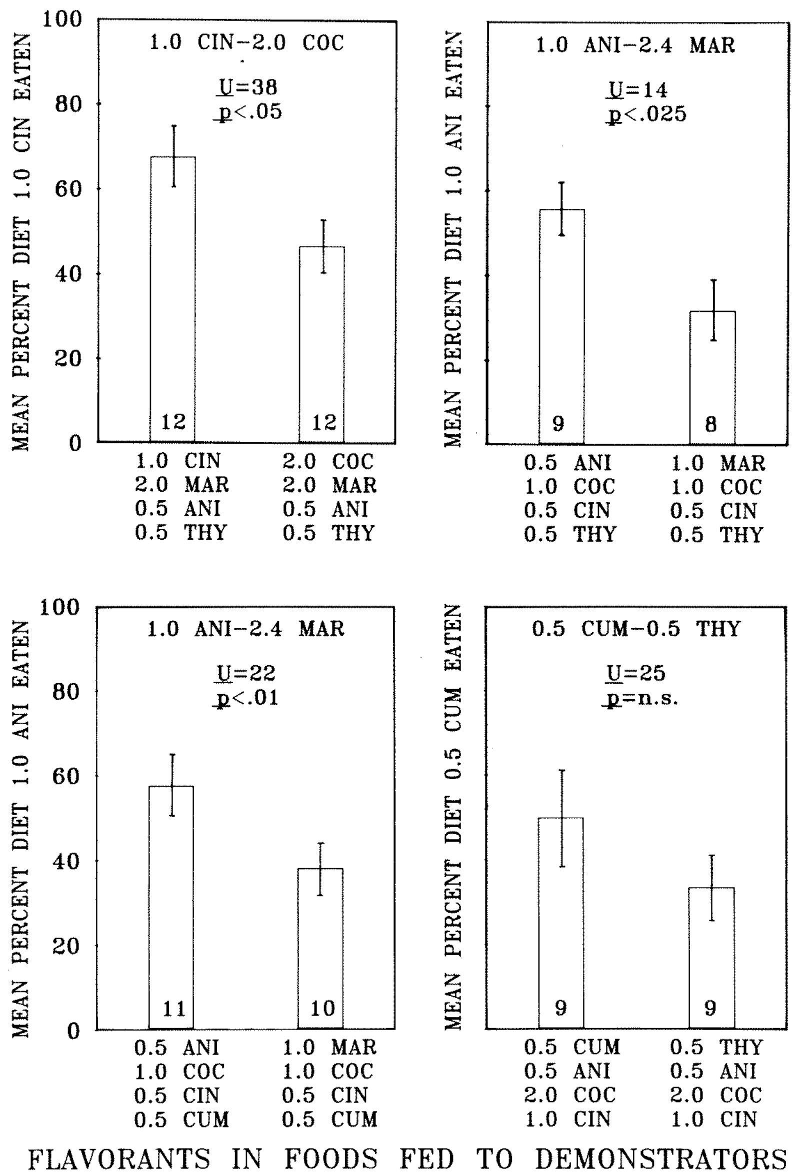

Figure 2. The four panels show the mean amount of Diet 1.0 Cin, 1.0 Ani, or 0.5 Cum eaten by observers that had interacted with demonstrators fed four-flavored foods during Step 2 of Procedure (Experiment 1). The choice of diets offered to each group of subjects is indicated by the floating title above each pair of histograms; the flavorants in the foods fed to each group of demonstrators are shown below each histogram. The numbers in each histogram = *n*/group. Flags = ±1 *SEM*.

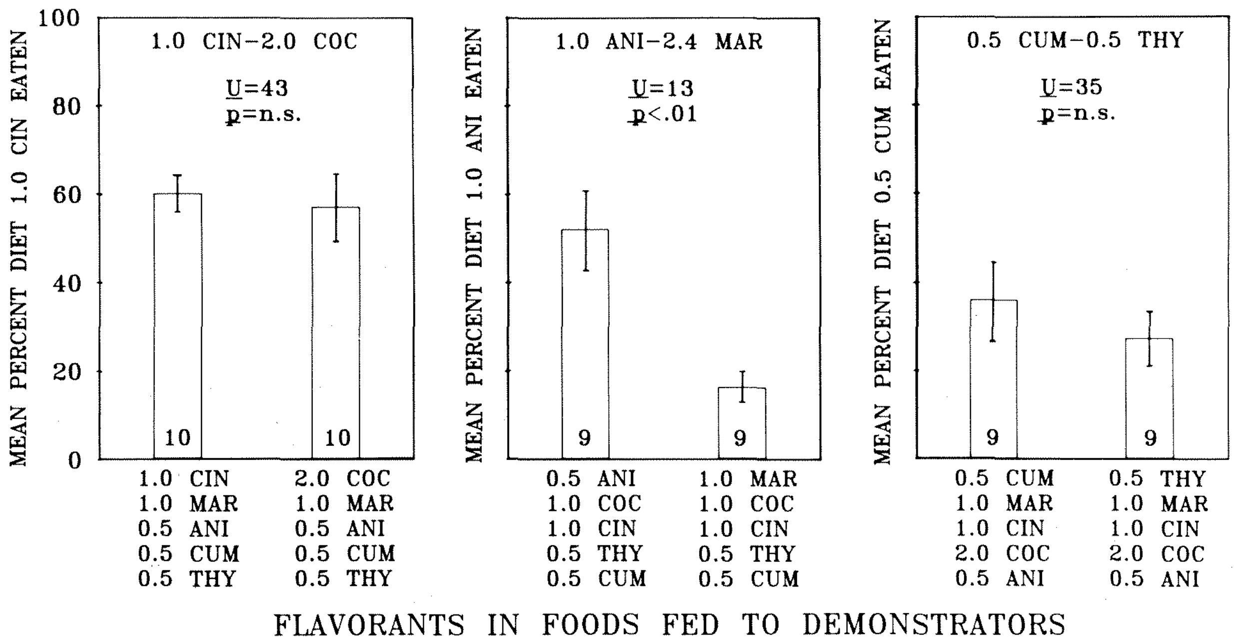

Figure 3. The three panels show the mean amount of Diet 1.0 Cin, 1.0 Ani, or 0.5 Cum eaten by observers that had interacted with demonstrators fed five-flavored foods during Step 2 of Procedure (Experiment 1). The choice of diets offered to each group of subjects is indicated by the floating title above each pair of histograms; the flavorants in the foods fed to each group of demonstrators are shown below each histogram. The numbers in each histogram = *n*/group. Flags = ±1 *SEM*.

to their respective demonstrators during Step 2. Each panel within each figure indicates the amount of Diet 1.0 Cin, Diet 1.0 Ani, or Diet 0.5 Cum eaten by observers as a percentage of their total intake during Step 4.

As is evident from an examination of Figures 1–3, and as statistical tests confirmed (Mann-Whitney *U* tests; see Figures 1–3 for *U* and *p* values), the observers in both Study 1 (those observers that interacted with demonstrators fed a three-flavored diet) and Study 2 (those observers that interacted with demonstrators fed a four-flavored diet) (1) showed a greater preference for Diet 1.0 Cin after interacting with a demonstrator that had eaten a multiflavored diet containing Cin than after interacting with a demonstrator that had eaten a multiflavored diet containing Coc and (2) showed a greater preference for Diet 1.0 Ani after interacting with a demonstrator that had eaten a multiflavored diet containing Ani than after interacting with a demonstrator that had eaten a multiflavored diet containing Mar. Although the observers in Study 2 that interacted with a demonstrator fed a multiflavored diet that contained Cum exhibited a greater preference for Diet 0.5 Cum during testing than did the observers that interacted with a demonstrator fed a multiflavored diet that contained Thy, the difference was not statistically significant (critical value of $U = 21$).

In most cases, as can be seen in Figure 3, observers in Study 3 (those observers that interacted with demonstrators that had eaten a five-flavored diet) did not exhibit enhanced preferences for the flavorants added to the diets that their respective demonstrators had eaten. Although those observers whose demonstrators had eaten a multiflavored diet containing either Ani or Mar exhibited enhanced food preferences during testing that positively correlated with the diet that their respective demonstrators had eaten, those observers whose demonstrators had eaten a multiflavored diet containing either (1) Cin or Coc or (2) Cum or Thy did not do so.

In sum, the results of the present experiments repeat the demonstration in Galef et al. (1990) that observer rats can detect three different flavorants eaten by a demonstrator and, in addition, indicate that as the number of flavorants eaten by a demonstrator increases, the probability of an observer extracting usable diet-related information from that demonstrator decreases.

EXPERIMENT 2

In Experiment 1, as in most other published studies of social transmission of food preference by rats (for review, see Galef, 1986, 1988), one of a pair of subjects was fed an unfamiliar diet and acted as a demonstrator, whereas the second member of each pair of subjects was an experimentally naive individual (an observer) that extracted diet-identifying information from its demonstrator partner. As mentioned in the introduction to the present paper, it has recently been reported (Galef, 1991) that, during a single period of interaction, each member of a pair of interacting rats can act both as a demonstrator and as an observer, providing diet-identifying information to, and extracting diet-identifying information from, its partner.

In Experiment 2, we examined the ability of interacting rats to exchange information about multiflavored diets. Each rat in those pairs of rats assigned to one of four experimental conditions first ate a four-flavored food and then interacted with a partner that had eaten a different four-flavored food. Finally, each rat was offered a choice between two different single-flavored foods. One of the two single-flavored foods offered to each subject had a flavor that was a component of the four-flavored food that the subject had eaten. The other single-flavored food offered each subject had a single flavor that was a component of the four-flavored food which that subject's partner had eaten.

To determine whether any effects on food choices of the subjects during testing were the result of the interaction of subjects with their respective partners, rather than the result of direct ingestion of a four-flavored food, the members of each of eight groups of control subjects ate a four-flavored food, did not interact with a partner, and were then offered a choice between one of the pairs of single-flavored foods that had been offered subjects in one of the four experimental groups.

Method

Subjects. One hundred forty-eight 42-day-old Long-Evans rats, born in the vivarium of the McMaster University Psychology Department to breeding stock acquired from Charles River Canada (St. Constant, Quebec), served as subjects. The subjects were assigned to 1 of 16 groups that differed in (1) the foods that they ate during Step 1 of Procedure (either Combination A or Combination B), (2) whether they interacted with another subject during Step 3, and (3) which of four pairs of diets they were offered during Step 4.

Foods. During Step 2, each subject was fed one of two four-flavored foods, either Combination A ([in grams per 100 g of diet] 97.5 powdered Purina Rodent Laboratory Chow 5001, 1.0 cinnamon, 0.5 anise, 0.5 thyme, and 0.5 ground cloves [Clo]) or Combination B ([in grams per 100 g of diet] 96.0 powdered Purina Rodent Laboratory Chow 5001, 2.0 cocoa, 1.0 marjoram, 0.5 cumin, and 0.5 ground rosemary [Ros]).

During Step 4, each subject was offered one of the following four pairs of diets: (1) Diet 1.0 Cin and Diet 2.0 Coc, (2) Diet 0.5 Ani and Diet 1.0 Mar, (3) Diet 0.5 Thy and Diet 0.5 Cum, and (4) Diet 0.5 Clo and Diet 0.5 Ros. Note that each of these four pairs of diets consists of one diet containing a flavor present in Combination A and one diet containing a flavor present in Combination B.

Procedure. The experiment was carried out in four steps:

Step 1. Each experimentally naive, 42-day-old subject was established in a separate wire-mesh, hanging cage (24 × 19 × 18 cm) and placed on a 23-h/day food-deprivation schedule, eating powdered Purina Rodent Laboratory Chow 5001 for 1 h/day for 2 consecutive days.

Step 2. Following a third 23-h period of food deprivation, each subject was offered, for 1 h, a weighed food bowl containing either Combination A or Combination B.

Step 3. Immediately after the food bowl containing either Combination A or Combination B was removed from each subject's cage, subjects (n = 84) in eight experimental groups were placed in pairs, each pair composed of one subject that had eaten Combination A and one subject that had eaten Combination B, and were then left to interact freely for 30 min. During this 30-min period, subjects (n = 64) in each of eight control groups were left undisturbed in their home cages.

Step 4. At the end of Step 3, those 42 subjects in experimental groups that had been moved to the cage of another subject during Step 3 were returned to their own home cages, and each of the 148 subjects in the experiment was offered, for 22 h, one of the four pairs of diets described above.

The experimenter determined the amount of food eaten by each subject during both Steps 2 and 4.

Results and Discussion

The main results of Experiment 2 are presented in Figure 4, which shows the mean percentage of each subject's total intake during Step 4 that was the diet with a flavorant from Combination A (e.g., Cin, Ani, Thy, or Clo). As can be seen in Figure 4, and as statistical tests confirmed (Mann-Whitney U tests; see Figure 4 for U and p values), during Step 4, subjects in experimental groups (i.e., those subjects that had interacted with a partner during Step 3) exhibited enhanced preferences for the diets containing each of the four flavors in the food (Combination A or B) that their respective partners had eaten during Step 2.

On the other hand, during Step 4, the subjects in control groups (i.e., those subjects that had not interacted with partners during Step 3) did not exhibit differences in diet preference as a function of the four-flavored food that they had eaten themselves during Step 2 (Mann-Whitney U tests; see Figure 2 for U and p values). This finding, that exposure to a demonstrator rat that has eaten a food enhances observer rats' later preferences for that food, whereas eating the same food does not enhance rats' preferences for it, is common in experiments of this type (Galef, 1986, 1989; Heyes & Durlach, 1990).

To look more closely at the effects of social interaction with partners on subjects' diet preferences, we compared the diet choices, during Step 4, of the subjects in each experimental group with the diet choices of the subjects in those two control groups offered the same diet choice during Step 4. Thus, for each of the four panels in Figure 4, we compared the food choices of each of the two experimental groups (indicated by the two histograms to the left of each panel) with the food choices of the combined control groups (indicated by the large shaded histogram to the right of each panel).

We found that (1) subjects in experimental groups that ate Combination A and interacted with partners that had eaten Combination B ate significantly smaller percentages of Diet Cin, Diet Ani, and Diet Clo (Mann-Whitney U tests, all $ps < .05$), but not of Diet Thy (Mann-Whitney U test, $U = 51$, p = n.s.), than did subjects in their corresponding combined control groups and (2) subjects in experimental groups that ate Combination B and interacted with subjects that had eaten Combination A ate significantly larger percentages of Diets 1.0 Ani, 0.5 Clo, and 0.5 Thy (Mann-Whitney U tests, all $ps < .05$), but not of Diet Cin (Mann-Whitney U test, $U = 100$, p = n.s.), than did the subjects in corresponding combined control groups.

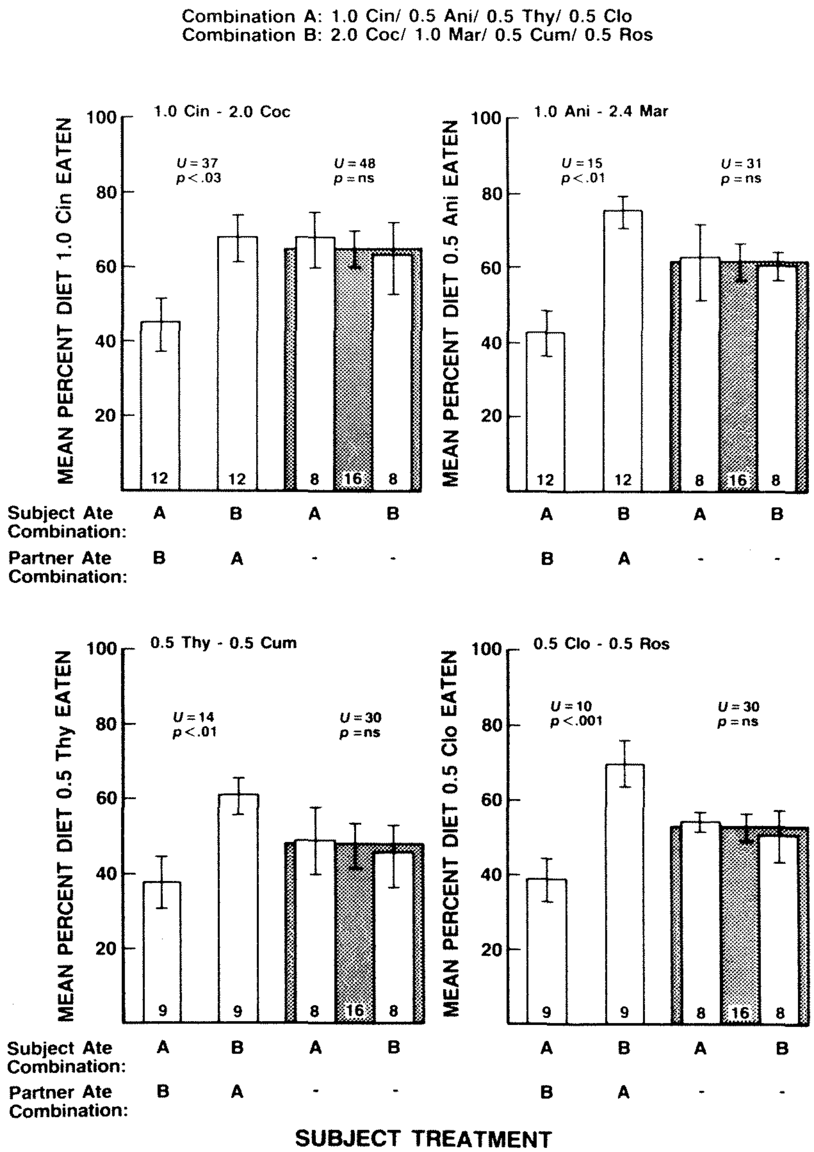

Figure 4. Each of the four panels shows the percentage of Diet 1.0 Cin, Diet 0.5 Ani, Diet 0.5 Thy, or Diet 0.5 Clo eaten during Step 4 of Procedure (Experiment 2) by subjects in experimental and control groups. The flavorants present in Combinations A and B are shown above the figure; the choice of diets offered to each group of subjects is indicated by the floating title above each panel. The shaded histograms indicate the combined mean for each pair of control groups; the numbers in each histogram = *n*/group. Flags = ±1 *SEM*.

In sum, our data indicate that the subjects in Experiment 2 were able to identify some, but not all, of the four flavors added to the four-flavored diets that their respective partners had eaten. This performance by experimental subjects, though not perfect, was impressive, especially given the presence of 11 substances in Purina Rodent Laboratory Chow 5001 at concentrations above 1% (D. Hopkins, personal communication, June 26, 1989), some of which (e.g., fish meal, molasses, brewer's yeast, meat meal, animal fat, etc.) are odoriferous and might have masked the odors of the eight flavorants used in the experiment.

GENERAL DISCUSSION

The results of the present series of experiments indicate that Norway rats are able to detect several different flavors simultaneously present in the diet of a conspecific: (1) A naive observer rat can reliably detect each of three or four different flavorants added to Purina chow that has been eaten by a conspecific demonstrator, and (2) pairs of rat subjects can exchange information about several different flavorants simultaneously present in Purina chow.

Of course, the number of flavorants a rat can detect during interaction with a conspecific should depend on the relative strengths of the odors of those flavorants as well as on the strength of the odor of the food to which flavorants have been added. Consequently, it is impossible to extrapolate from the present data to estimate the complexity of diet-identifying information rats could exchange when eating natural foods outside the laboratory. It does, however, seem safe to suggest, even on the basis of the present limited data, that (1) rats can extract useful information from conspecifics that have eaten more than one food and (2) the greater the number of foods a rat has eaten, the less reliably conspecifics can extract diet-identifying information from it.

The ability of rats to detect traces of several different foods eaten by a conspecific would be important to Norway rats living outside the laboratory if, when foraging, rats ate several different foods before returning to their burrows and interacting with conspecifics. Unfortunately, we have not been able to find any detailed analyses in the published literature of the stomach contents of wild Norway rats (*Rattus norvegicus*) living in undisturbed habitat. However, Clark (1980, 1981, 1982) has published descriptions of the stomach contents of black rats (*Rattus rattus*), which are congeners of Norway rats and are dietary generalists occupying tropical niches similar to those occupied by Norway rats in more temperate areas (Brown, 1960). The stomachs of these black rats typically contained four to six different foods in amounts greater than 1% of stomach content volume and an average of 2.7 "trace items," each contributing less than 1% to stomach content volume (Clark, 1982, p. 765). If Norway rats feed similarly to black rats, then the ability to determine what foods conspecifics have eaten, even when those conspecifics have eaten several different foods, might well be useful in natural circumstances.

It also seems reasonable to propose that in nature, as in the laboratory, the reliability with which Norway rats can extract diet-identifying information from conspecifics decreases with an increase in the number of foods that conspecifics have eaten (see Experiment 1). If so, a rat with much to gain from informing others about the foods that it has eaten (e.g., a female with weaning young) should exhibit a pattern of sampling among different foods while foraging that would be quite different from that of a rat with little or nothing to gain from successful communication of dietary information to conspecifics. It will be interesting to see whether Norway rats in the laboratory do, in fact, alter their patterns of food sampling in accord with their interests in successfully communicating with conspecifics.

REFERENCES

Brown, R. Z. (1960). *Biological factors in domestic rodent control.* Atlanta: U.S. Department of Health, Education and Welfare, Public Health Service, Communicable Disease Center.

Clark, D. A. (1980). Age- and sex-dependent foraging strategies of a small mammalian omnivore. *Journal of Animal Ecology*, **49**, 549-563.

Clark, D. A. (1981). Foraging patterns of black rats across a desert-montane forest gradient in the Galapagos Islands. *Biotropica*, **13**, 182-194.

Clark, D. A. (1982). Foraging behavior of a vertebrate omnivore (*Rattus rattus*): Meal structure, sampling, and diet breadth. *Ecology*, **63**, 763-772.

Galef, B. G., Jr. (1986). Olfactory communication among rats of information concerning distant diets. In D. Duvall, D. Muller-Schwarze, & R. M. Silverstein (Eds.), *Chemical signals in vertebrates: Vol. 4. Ecology, evolution, and comparative biology* (pp. 487-505). New York: Plenum.

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. 119-139). Hillsdale, NJ: Erlbaum.

Galef, B. G., Jr. (1989). Enduring social enhancement of rats' preferences for the palatable and the piquant. *Appetite*, **13**, 91-92.

Galef, B. G., Jr. (1991). Information centres of Norway rats: Sites for information parasitism and information exchange. *Animal Behaviour*, **41**, 295-301.

Galef, B. G., Jr., Attenborough, K. S., & Whiskin, E. E. (1990). Responses of observer rats to complex, diet-related signals emitted by demonstrator rats. *Journal of Comparative Psychology*, **104**, 11-19.

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.

Grover, C. A., Kixmiller, J. S., Erickson, C. A., Becker, A. H., Davis, S. F., & Nallan, G. B. (1988). The social transmission of information concerning aversively conditioned liquids. *Psychological Record*, **38**, 557-566.

Heyes, C. M., & Durlach, P. J. (1990). "Social blockade" of taste aversion learning in Norway rats (*R. norvegicus*): Is it a social phenomenon? *Journal of Comparative Psychology*, **104**, 82-87.

Posadas-Andrews, A., & Roper, T. J. (1983). Social transmission of food preferences in adult rats. *Animal Behaviour*, **31**, 265-271.

(Manuscript received May 16, 1991;
revision accepted for publication August 14, 1991.)