Anim. Behav., 1993, **46**, 257–265

Functions of social learning about food: a causal analysis of effects of diet novelty on preference transmission

BENNETT G. GALEF, JR
Department of Psychology, McMaster University, Hamilton, Ontario, L8S 4K1 Canada

(Received 4 March 1992; initial acceptance 12 March 1992; final acceptance 22 July 1992; MS. number: A6311)

Abstract. A naive rat (an observer) that interacts with a recently fed conspecific (a demonstrator) subsequently exhibits a substantially enhanced preference for whatever food its demonstrator ate. In the present series of experiments, it was found that: (1) demonstrator rats that ate foods unfamiliar to their respective observers influenced the food preferences of observers more than did demonstrator rats that ate foods familiar to their observers and (2) demonstrator rats that had eaten both a food unfamiliar to observers and a food familiar to observers induced greater preference for the former than for the latter. These results suggest that social enhancement of flavour preferences does not reinforce rats' inherent tendency to prefer familiar foods. Rather, social enhancement of flavour preference biases rats to incorporate unfamiliar foods into their feeding repertoires. Because (1) unfamiliar substances that conspecifics are eating are more likely to be beneficial than are other unfamiliar substances in the environment and (2) social interaction increases the probability that rats will ingest unfamiliar substances that conspecifics are eating, socially induced changes in diet preference should reduce potential costs of increasing dietary breadth.

In a series of studies extending over more than a decade, my co-workers and I have demonstrated repeatedly that Norway rats, *Rattus norvegicus*, can influence one another's food preferences (for reviews see, Galef 1989a, 1990). The effects of interaction with demonstrators on the food preferences of their observers are profound: social interaction can reverse both learned aversions (Galef 1986) and congenital flavour preferences (Galef 1989b). Socially enhanced food preferences persist for weeks after their induction (Galef 1989b; Galef & Kennett 1985; Winocur 1990), and social induction of food preference occurs under a broad range of experimental conditions (Galef et al. 1984). The robustness of social influences on food choices of captive rats suggests that socially acquired information can play an important role in the development of adaptive patterns of food selection by rats living in natural habitats.

Of course, social influence is but one of several factors that can affect the food preferences and feeding repertoires of rats. An individual's congenital hedonic responses to the flavours of foods (Young 1959), its familiarity with the tastes of foods (Siegel 1974) as well as its experience of the post-ingestional consequences of eating foods (Garcia & Koelling 1966; Booth 1985) can each contribute to development of flavour preferences.

Although there is abundant evidence in the literature both of the effects of individual experiences and of social influences on the food choices of rats, considerable uncertainty remains as to how socially acquired information concerning foods might be integrated with an individual's own experience of foods in shaping food preferences and resultant feeding repertoires. The experiments described here were undertaken to examine interaction of the familiarity of foods (a result of individual experience) with social induction of preference for foods.

The literature describing the feeding habits of wild Norway rats (the population in which the foraging strategies of domesticated Norway rats evolved) indicates that wild rats are intensely conservative in their food choices (Rzoska 1953; Barnett 1958; Galef 1970). A captive wild rat will wait as long as 5 days before eating an unfamiliar food introduced into its home cage (Galef 1970), even when no familiar foods are available there, and this delay in ingesting the available unfamiliar food results in self starvation. Indeed, much of the reputed cleverness of Norway rats in avoiding poison baits may be a consequence of their hesitancy to eat foods that they have not previously eaten (Shorten 1958; Barnett 1975; Meehan 1984).

This reluctance of wild rats to ingest unfamiliar substances probably reflects risks inherent in

0003–3472/93/080257+09 $08.00/0

sampling unfamiliar potential foods (Rozin 1976). There is always a chance that an unknown potential food either contains toxic secondary compounds or has no nutritive value. Because of such potential costs of sampling unfamiliar substances, any behavioural process should be favoured that increases the probability that rats would sample safe, nutritious foods when attempting to expand their dietary repertoires.

It seems reasonable to suppose that unfamiliar substances that conspecifics are eating are relatively unlikely to be either noxious or without nutritive value. It, therefore, seems likely that a tendency to sample preferentially those unfamiliar substances that conspecifics are already eating would reduce costs inherent in tasting unfamiliar substances.

If, in fact, socially induced enhancement of food preference is a behavioural process that has evolved to permit dietary generalists to expand their feeding repertoires without incurring some of the costs inherent in sampling previously untasted potential foods, then one might expect social exposure to unfamiliar foods to be more effective than social exposure to familiar foods in altering food preferences. The first experiment was undertaken to test the hypothesis that rats are especially susceptible to social enhancement of their preferences for unfamiliar foods.

EXPERIMENT 1

In the present experiment, each member of two groups of naive rats (observers) was exposed to a conspecific demonstrator that had recently eaten a food that contained two flavours: flavour A and flavour B. Members of one group of observer rats were familiar with flavour A, while members of the other group were familiar with flavour B. After each member of both groups of observers had interacted with a demonstrator that had eaten a food containing both flavour A and flavour B, the observers were offered a choice between a diet containing flavour A and a diet containing flavour B.

Based on the argument presented in the introduction, one might expect that, in the choice situation, those observer rats familiar with flavour A prior to this interaction with a demonstrator that had eaten both flavour A and flavour B would prefer flavour B, and those observer rats familiar with flavour B would prefer flavour A. This expectation runs counter to what one might predict on other grounds. For eample, because rats are hesitant to eat foods with unfamiliar tastes, it might be argued that rats familiar with flavour A would prefer flavour A to flavour B in a choice situation and that experience with a demonstrator that had eaten a food containing both flavours A and B should only strengthen the preference for flavour A of rats already familiar with that flavour. The outcome of experiment 1 is not a foredrawn conclusion.

Methods

Subjects

Thirty-two experimentally naive, 42-day-old, female, Long–Evans rats, born in the vivarium of the McMaster University Psychology Department (Hamilton, Ontario, Canada) to breeding stock descended from animals acquired from Charles River Canada (St Constant, Quebec, Canada), served as observers. Before the start of the experiment, we maintained these observers with ad libitum access to pellets of Purina Rodent Laboratory Chow No. 5001 and water in groups of three or four littermates of the same sex in polycarbonate, shoe-box cages measuring 35 × 30 × 15 cm. An additional 32, 49- to 56-day-old female rats, which had served as observers in previous experiments, served as demonstrators in the present experiment.

Diets

Six different diets were made by adding four flavourants (cinnamon: Cin, cocoa: Coc, marjoram: Mar, and anise: Ani), either singly or in pairs, to powdered Purina Rodent Laboratory Chow No. 5001. For example, a diet composed by adding 1·0 g of cinnamon to 99 g of chow is referred to as Diet 1·0 Cin and a diet composed by adding both 1·0 g of cinnamon and 2·0 g of cocoa to 97 g of chow as Diet 1·0 Cin/2·0 Coc. The six diets used in the present experiment were: Diet 1·0 Cin, Diet 2·0 Coc, Diet 1·0 Cin/2·0 Coc, Diet 1·0 Ani, Diet 1·0 Mar and Diet 1·0 Ani/1·0 Mar.

Apparatus

Demonstrators and observers were each housed individually throughout the 4 days of the experiment in wire-mesh hanging cages measuring 18 × 34 × 19 cm.

Procedure

I randomly assigned each observer and each demonstrator to one of two conditions; treatment of subjects in the two conditions differed only in the foods that they were offered. I offered subjects in condition 1 (16 observers and 16 demonstrators), Diets 1·0 Cin, 2·0 Coc and 1·0 Cin/2·0 Coc and subjects in condition 2 (16 observers and 16 demonstrators) Diets 1·0 Ani, 1·0 Mar and 1·0 Ani/1·0 Mar.

The experimental procedure involved the three steps described below. (1) To begin the experiment, I fed each of the 16 observers in condition 1 either Diet 2·0 Coc ($N=8$) or Diet 1·0 Cin ($N=8$) ad libitum for 3 consecutive days, and I fed each of the 16 observers in condition 2 either Diet 1·0 Ani ($N=8$) or Diet 1·0 Mar ($N=8$) for a similar period. While observers were eating either Diet 1·0 Cin, 2·0 Coc, 1·0 Mar or 1.0 Ani, I placed all 32 demonstrators on a 23 h/day food-deprivation schedule, eating powdered Purina Rodent Laboratory Chow for 1 h/day for 2 consecutive days. Following a third 23-h period of food deprivation, I fed each of the 16 demonstrators assigned to condition 1 Diet 1·0 Cin/2·0 Coc for 1 h and each of the 16 demonstrators assigned to condition 2, Diet 1·0 Ani/1·0 Mar for 1 h. (2) At the end of each demonstrator's 1-h feeding period, I removed all food from observers' cages and placed each demonstrator in the home cage of an observer rat assigned to the same condition as that demonstrator. Demonstrator and observer were then left to interact freely for 30 min. (3) At the end of the 30-min period of interaction between demonstrators and observers. I removed demonstrators from the experiment and offered each observer in condition 1 a choice between weighed quantities of Diet 1·0 Cin and Diet 2·0 Coc. At the same time, I offered each observer in condition 2 a choice between weighed quantities of Diet 1·0 Ani and Diet 1·0 Mar.

Twenty-two hours later, I determined the amount of each diet eaten by each observer.

Results and Discussion

The main results of experiment 1 are presented in Fig. 1, which shows the mean amount of Diet 1·0 Cin eaten during testing by observers in condition 1, expressed as a percentage of the total amount that those observers ate during the 22-h test period (Fig. 1a), and the mean amount of Diet 1·0 Ani eaten during testing by observers in condition 2,

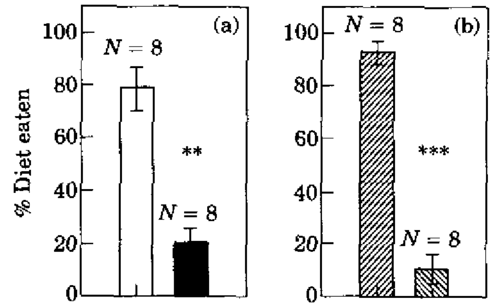

Figure 1. Mean ($\pm$SE) percentage of cinnamon-flavoured diet eaten during testing by observers in condition 1 of experiment 1 that were familiar with either the cinnamon- (■) or cocoa-flavoured (□) diet. (b) Mean ($\pm$SE) percentage of anise-flavoured diet eaten during testing by observers in condition 2 that were familiar with either the anise- (▧) or marjoram-flavoured (▨) diet. $^{**}P<0{\cdot}001$, $^{***}P<0{\cdot}0001$ (Mann–Whitney U, see text for details).

expressed as a percentage of the total amount that those observers ate during the 22-h test period (Fig. 1b). During testing, observers ate more of the unfamiliar diet that their respective demonstrators had eaten than of the familiar flavour diet (Mann–Whitney U-tests, condition 1: $U=2$, $P<0{\cdot}001$; condition 2: $U=0$, $P<0{\cdot}0001$).

The finding that observer rats eat more of an unfamiliar than of a familiar food eaten by their respective demonstrator is consistent with the hypothesis that a primary function of social enchancement of food preference in rats is to induce individuals to expand their feeding repertoires to include unfamiliar foods that conspecifics are eating.

EXPERIMENT 2

The results of experiment 1, though consistent with the hypothesis that prior exposure to a flavour interferes with subsequent social enhancement of preference for that flavour, can also be interepted as showing only that rats will eat more of a novel food than of a familiar one. Experiment 2 was undertaken to provide evidence that familiarity with a food interferes directly with social enhancement of preference for that food.

In the present experiment, each observer rat first became familiar with one of three diets. It then interacted with a demonstrator rat fed both the diet that the observer had eaten and a second diet unfamiliar to the observer. Finally, each observer was given a choice among the three diets: the two that its demonstrator had eaten previously (one familiar and one unfamiliar to the observer) and the one that neither the observer nor its demonstrator had eaten previously. If prior exposure to a diet interfered with social induction of diet preference, one would expect to see observers eat more of the unfamiliar diet eaten by their respective demonstrators than of either (1) the diet eaten by demonstrators that was familiar to observers or (2) the totally unfamiliar diet.

Methods

Subjects

Thirty experimentally naive, 42-day-old, female Long–Evans rats from the vivarium of the McMaster University Psychology Department served as observers. An additional 30, 49- to 56-day-old female rats served as demonstrators.

Diets

Six different diets were composed by adding ground cinnamon, cocoa and anise to powdered Purina Rodent Laboratory Chow. Using the notation introduced in Methods of experiment 1, these six diets may be described as Diet 1·0 Cin, Diet 2·0 Coc, Diet 1·0 Ani, Diet 1·0 Cin/2·0 Coc, Diet 1·0 Cin/1·0 Ani and Diet 2·0 Coc/1·0 Ani.

Apparatus

The apparatus used in experiment 2 was the same as that used in experiment 1.

Procedure

Five observers and five demonstrators were assigned to each of six experimental conditions that differed only in the foods offered to subjects.

To begin the experiment, I fed 10 observers Diet 1·0 Cin, 10 observers Diet 2·0 Coc and 10 observers Diet 1·0 Ani ad libitum for 3 consecutive days. While observers were becoming familiar with their respective diets, I placed all 30 demonstrators on a 23-h/day food-deprivation schedule, eating powdered Purina Rodent Laboratory Chow for 1 h/day for 2 consecutive days. Following a third 23-h period of food deprivation, I fed 10 demonstrators Diet 1·0 Cin/2·0 Coc, 10 demonstrators Diet 1·0 Cin/1·0 Ani and 10 demonstrators Diet 2·0 Coc/1·0 Ani. I then placed each demonstrator in the cage of an observer and allowed demonstrator–observer pairs to interact for 30 min. The 10 observers that had eaten Diet 1·0 Cin interacted either with demonstrators that had eaten either Diet 1·0 Cin/2·0 Coc or Diet 1·0 Cin/1·0 Ani; the 10 observers that had eaten Diet 2·0 Coc interacted with demonstrators that had eaten either Diet 1·0 Cin/2·0 Coc or Diet 2·0 Coc/1·0 Ani, and the 10 observers that had eaten Diet 1·0 Ani interacted with demonstrators that had eaten either Diet 1·0 Cin/1·0 Ani or Diet 2·0 Coc/1·0 Ani.

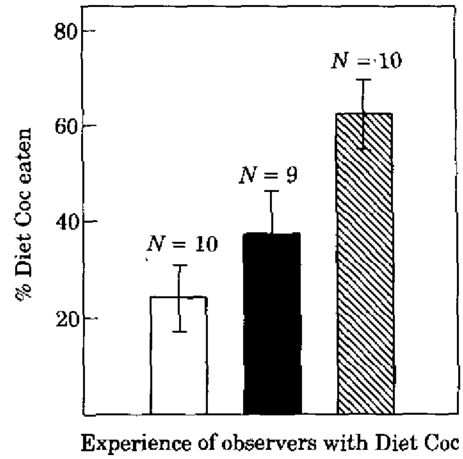

Figure 2. Mean (±SE) percentage of Diet Coc eaten during testing by observers in experiment 2 when Diet Coc was a totally unfamiliar diet (□), a familiar diet eaten by a demonstrator (■) and an unfamiliar diet eaten by a demonstrator (▨).

I removed the demonstrators from each observers cage and offered each observer a choice among weighed samples of Diet 1·0 Cin, 2·0 Coc and 1·0 Ani. Thus, each subject could choose among: (1) a familiar diet that its demonstrator had eaten, (2) an unfamiliar diet that its demonstrator had eaten and (3) a totally unfamiliar diet.

Twenty-two hours later, the experimenter first determined both the amount of Diet 2·0 Coc and the total amount eaten by each observer during testing, and then calculated the percentage of each observer's total intake that was Diet 2·0 Coc.

Results and Discussion

The main results of experiment 2 are presented in Fig. 2, which shows the mean percentage of each observer's total intake during testing that was Diet

Coc when Diet Coc was: (1) the totally unfamiliar diet, (2) the familiar diet eaten by an observer's demonstrator and (3) the unfamiliar diet eaten by an observer's demonstrator. As is clear from inspection of Fig. 2, the observers' intake of Diet Coc during the 22-h test period varied as a function of their previous exposure to Diet Coc (Kruskal–Wallace one-way ANOVA, $H = 6{\cdot}90$, $P < 0{\cdot}05$). Observers ate a significantly greater amount of Diet Coc when Diet Coc was the unfamiliar diet eaten by their demonstrators than when Diet Coc was either the familiar diet eaten by their demonstrators or the totally unfamiliar diet (Mann–Whitney U-tests, both $Us < 18$, both $Ps < 0{\cdot}05$).

EXPERIMENT 3

Outside the laboratory, free-living Norway rats probably encounter not only individual conspecifics that have each eaten more than one food type, but also a succession of conspecifics that have each eaten different foods. In the present experiment, I inquired as to whether the food preferences of observer rats would be affected more by interaction with a conspecific that had eaten a food familiar to the observer than by interaction with a conspecific that had eaten a food unfamiliar to the observer.

Each of 24 observer rats first ate one of a pair of diets and then interacted with two demonstrator rats in succession. One of these demonstrators had eaten the same diet that its observer had eaten; the other demonstrator had eaten the second diet in the pair. Finally, I offered each observer a choice between the two diets that its demonstrators had eaten.

Methods

Subjects

Twenty-four experimentally naive, 42-day-old, female Long–Evans rats from the McMaster Psychology Department vivarium served as observers. An additional 48, 49- to 56-day-old female rats, which had served as observers in previous experiments, served as demonstrators in the present experiment.

Diets

Four different diets were composed by adding ground cinnamon, cocoa, marjoram and anise to powdered Purina Rodent Laboratory Chow. Using the notation introduced in Methods of experiment 1, these four diets may be described as Diet 1·0 Cin, Diet 2·0 Coc, Diet 1·0 Ani and Diet 1·0 Mar.

Apparatus

The apparatus used in experiment 2 was the same as that used in experiment 1.

Procedure

Again, I randomly assigned observers and demonstrators to one of two conditions that differed only in the flavours of the food offered to subjects. In condition 1 (12 observers and 24 demonstrators), I offered Diet 1·0 Cin and 2·0 Coc to subjects, while in condition 2 (12 observers and 24 demonstrators), I used Diets 1·0 Ani and 1·0 Mar.

The experimental procedure involved the four steps described below.

(1) To begin the experiment, I fed each of the 12 observers in condition 1 either Diet 2·0 Coc ($N = 6$) or Diet 1·0 Cin ($N = 6$) ad libitum for 3 consecutive days and each of the 12 observers in condition 2 either Diet 1·0 Ani ($N = 6$) or Diet 1·0 Mar ($N = 6$) for a similar period. While observers were becoming familiar with their respective diets, I placed all 48 demonstrators on a 23-h/day food-deprivation schedule, eating powdered Purina Rodent Laboratory Chow for 1 h/day for 3 consecutive days. Following the third 23-h period of food deprivation, 12 of the 24 demonstrators that had been assigned to condition 1 were fed Diet 1·0 Cin, while the remaining 12 demonstrators were fed Diet 2·0 Coc. At the same time, 12 of the 24 demonstrators assigned to condition 2 were fed Diet 1·0 Ani while the 12 remaining demonstrators were fed Diet 1·0 Mar.

(2) At the end of the 1-h period of demonstrator feeding, I placed the six demonstrators that had been fed Diet 1·0 Cin and the six demonstrators that had been fed Diet 2·0 Coc individually into the home cages of the 12 observers assigned to condition 1. At the same time, I placed the six demonstrators that had been fed either Diet 1·0 Ani or Diet 1·0 Mar individually into the home cages of the 12 observers assigned to condition 2. Observers and demonstrators were then left undisturbed for 15 min.

(3) At the end of step 2, I removed demonstrators from their observers' cages and replaced them with a second group of demonstrators. Each observer in condition 1 that had interacted during step 2 with a

demonstrator fed Diet 2·0 Coc interacted during step 3 (for 15 min) with a demonstrator that had eaten Diet 1·0 Cin and vice versa. Each observer in condition 2 that had interacted during step 2 with a demonstrator fed Diet 1·0 Ani interacted for 15 min with a demonstrator that had eaten Diet 1·0 Mar and vice versa.

I scheduled interactions of observers with demonstrators in condition 1 so that half the observers interacted first (in step 2) with a demonstrator fed Diet 1·0 Cin, and half of the observers interacted with a demonstrator fed Diet 2·0 Coc. Similarly, in condition 2, I counterbalanced the order of presentation of demonstrators fed Diet 1·0 Ani and 1·0 Mar to observers across subjects.

(4) At the end of the second 15-min period of interaction between demonstrators and their respective observers, I removed all demonstrators from observers' cages, and offered (a) each observer in condition 1 a choice between weighed quantities of Diets 1·0 Cin and 2·0 Coc and (b) each observer in condition 2 a choice between weighed quantities of Diets 1·0 Ani and 1·0 Mar.

Twenty-two hours later, I determined the amount of each diet eaten by each observer.

Results and Discussion

The main results of experiment 3 are presented in Fig. 3 which shows, the mean amount of Diet 1·0 Cin eaten during testing by observers in condition 1, expressed as a percentage of the total amount that those observers ate during the 22-h test period (Fig. 3a) and the mean amount of Diet 1·0 Ani ingested during testing by observers in condition 2, expressed as a percentage of the total amount that those observers ate during the 22-h test period (Fig. 3c). During testing, observers ingested more of the unfamiliar diet eaten by their respective demonstrators than of the familiar diet (Mann–Whitney U-tests, condition 1: $U=0$, $P<0{\cdot}001$; condition 2: $U=1$, $P<0{\cdot}002$). For example, observers familiar with cinnamon-flavoured diet that interacted with both a demonstrator fed cinnamon-flavoured diet and a demonstrator fed cocoa-flavoured diet preferred cocoa-flavoured diet, while the converse was true of observers familiar with cocoa-flavoured diet. Clearly, the food preferences of observers were more affected by interaction with a demonstrator that had eaten an unfamiliar food than by interaction with a demonstrator that had eaten a familiar food.

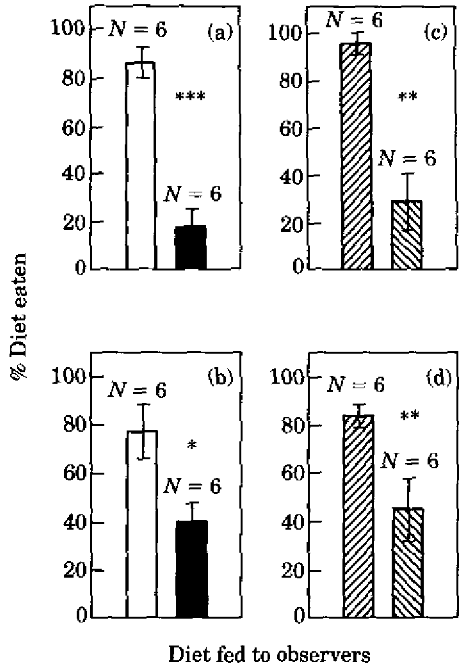

Figure 3. Mean (±SE) percentage of cinnamon-flavoured diet eaten during testing by observers in condition 1 that were familiar with either the cinnamon- (■) or cocoa-flavoured (□) diet in (a) experiment 3 and (b) experiment 4. The mean (±SE) amount of anise-flavoured diet eaten during testing by observers in condition 2, that were familiar with either the anise- (▧) or marjoram-flavoured (▨) diet in (c) experiment 3 and (d) experiment 4. $^*P<0{\cdot}02$, $^{**}P<0{\cdot}004$, $^{***}P<0{\cdot}001$ (Mann–Whitney U, see text for details).

EXPERIMENT 4

It might well be argued that the designs of experiments 1 and 2 are so great an oversimplification of feeding behaviour as it occurs in natural habitat that the result cannot be extrapolated with any confidence to behaviour outside the laboratory. Many free-living rats must eat more than one or two different foods in a feeding bout. Consequently, there is no reason to expect that principles demonstrated in rats maintained in the laboratory on very simple diets should apply to rats living outside the laboratory, which must eat complex diets to meet their nutrient needs.

The present experiment, like experiment 1, was undertaken to explore the relative effectiveness of familiar and unfamiliar foods eaten by demonstrators on the enhancement of their observers' food preferences. However, in experiment 4, unlike experiment 1, the diets of both demonstrators and observers were quite complex.

Demonstrators each ate a diet to which four flavours had been added, and each observer ate one of four different diets each of which contained three of the four flavours that were in the demonstrators' diet. I then looked to see whether observers exhibited enhancement of their preferences for the flavour in the diet that their demonstrator had eaten that was not present in the diet that observers had eaten.

Methods

Subjects

Twenty-four experimentally naive, 42-day-old, female Long–Evans rats born and reared in the vivarium of the McMaster University Psychology Department served as observers. An additional 24, 49- to 56-day-old, female Long–Evans rats, which had served as observers in previous experiments, served as demonstrators in the present experiment.

Diets

In addition to four of the diets used in both experiments 1 and 3 (Diets 1·0 Cin, 2·0 Coc, 1·0 Ani, 1·0 Mar), five complex diets were used in the present experiment. For example, a diet consisting of 95·5 g of powdered Purina Rodent Laboratory Chow to which had been added 1·0 g of ground cinnamon, 0·5 g of ground anise, 1·0 g of ground marjoram and 2·0 g of cocoa is described as Diet 1·0 Cin/0·5 Ani/1·0 Mar/2·0 Coc. The four new diets used in experiment 4 can be described as Diet 0·5 Ani/1·0 Mar/1·0 Cin, Diet 0·5 Ani/1·0 Mar/2·0 Coc, Diet 1·0 Cin/2·0 Coc/0·5 Ani and Diet 1·0 Cin/2·0 Coc/1·0 Mar.

Apparatus

The apparatus used in experiment 4 was the same as that used in preceding experiments.

Procedure

The procedure of the present experiment was identical to that of experiment 1, except in the diets that I fed to observers and demonstrators during steps 1 and 2 of procedure. In the present experiment, I fed observers in condition 1 either Diet 0·5 Ani/1·0 Mar/1·0 Cin (Combination A) or Diet 0·5 Ani/1·0 Mar/2·0 Coc (Combination B) for 3 days during step 1. Both Combination A and Combination B contained anise and marjoram; they differed only in that Combination A contained cinnamon while Combination B contained cocoa.

We fed observers in condition 2 either Diet 1·0 Cin/2·0 Coc/0·5 Ani (Combination C) or Diet 1·0 Cin/2·0 Coc/1·0 Mar (Combination D) during step 1. Both Combination C and Combination D contained cinnamon and cocoa; they differed only in that Combination C contained anise while Combination D contained marjoram.

During step 2, we fed all 24 demonstrators in the experiment Diet 1·0 Cin/0·5 Ani/1·0 Mar/2·0 Coc for 1 h before they interacted with an observer. Thus, as in experiment 1, each observer interacted with a demonstrator that had eaten a diet containing only one flavour that was unfamiliar to the observer.

Finally, during testing in step 3, I offered observers in condition 1a choice between Diets 1·0 Cin and 2·0 Coc for 22 h, and observers in condition 2 a choice between Diets 1·0 Mar and 1·0 Ani.

Results and Discussion

The main results of experiment 4 are again presented in Fig. 3, which shows the mean amount of Diet 1·0 Cin eaten during testing by observers in condition 1 (Fig. 3b), expressed as a percentage of the total amount that those observers ate during the 22-h test period and the mean amount of Diet 1·0 Ani eaten during testing by observers in condition 2 (Fig. 3d), expressed as a percentage of the total amount that those observers ate during the 22-h test period. During testing, observers in both conditions 1 and 2 exhibited a significant enhancement of their intake of the diet containing the unfamiliar flavourant that their respective demonstrators had eaten (Mann–Whitney U-tests, condition 1: $U=5$, $P<0.02$; condition 2: $U=2$, $P<0.004$). For example, observers in condition 1 that had been fed Combination A (which contained cinnamon) before they interacted with a demonstrator that had been fed a diet containing both cinnamon and cocoa, exhibited a preference for cocoa-flavoured diet during testing. On the other hand, observers in condition 1 that had been fed Combination B (which contained cocoa) exhibited a preference during testing for the cinnamon-flavoured diet after they interacted with a demonstrator that had been fed a diet containing both cinnamon and cocoa. Clearly, the food choices of observers eating fairly complex diets are influenced more by unfamiliar flavours than by familiar flavours in their respective demonstrator's diet.

It should, perhaps, be pointed out that subjects in all three experiments ate diets considerably more complex than might appear at first glance. Purina Rodent Laboratory Chow is itself composed of five major ingredients (ground corn, soybean meal, beet pulp, fish meal and ground oats), each comprising from 5 to 35% of the chow, and six additional ingredients (meat meal, dried whey, animal fat, molasses and alfalfa), each of which contributes more than 1% to the weight of the chow, as well as more than a dozen additional vitamins and minerals (D. Hopkins, personal communication). Subjects in experiment 4, familiar not only with Purina Chow, but also with three added flavours were detecting an unfamiliar flavour against a background of many familiar flavours present in the diet fed to their demonstrators.

GENERAL DISCUSSION

The results of the present series of experiments demonstrate that the food preferences of Norway rats are influenced more by exposure to unfamiliar elements in the diets of conspecifics than by exposure to familiar elements.

The significance of this finding for understanding the role of social interactions in the development of adaptive feeding repertoires in rats is, perhaps, most clearly communicated by considering implications of the opposite outcome. If rats were influenced more by exposure to familiar than to unfamiliar elements in the diets of conspecifics, then social influences on food preferences could be viewed as serving a primarily conservative function, increasing the tendency of rats to limit their intake to foods with which they were already familiar and which they knew to be safe. The present data, demonstrating that observer rats exhibit an enhanced probability of ingesting unfamiliar rather than familiar foods eaten by their respective demonstrators, suggest that social interactions serve primarily as a means of expanding feeding repertoires rather than of maintaining dietary conservatism.

In addition to casting some light on the function of socially induced diet preferences, the present data also suggest a previously unsuspected level of complexity in the functioning of rat colonies as information centres (Ward & Zahavi 1973; Galef & Wigmore 1983; Galef 1991). The food choices of young animals with relatively limited experience of foods should be biased, first in one direction, then another, as the result of chance encounters with conspecifics that have eaten various foods unfamiliar to the young. Their elders, already familiar with many of the foods available within their colony's home range, should be relatively insulated from such social impacts on their feeding behaviour. Only discovery of a new food source by some colony member would result in a renewed major impact of social interaction on the feeding preferences of experienced individuals.

ACKNOWLEDGMENTS

This research was supported by grants from the Natural Sciences and Engineering Research Council of Canada and the McMaster University Board. I thank Mertice Clark and Martin Daly for thoughtful comments on early drafts of the manuscript, Elaine Whiskin for technical assistance and Dr David Hopkins of Purina Mills Inc. (St Louis, Missouri) for sharing proprietary information concerning the manufacture of Purina Rodent Laboratory Chow No. 5001.

REFERENCES

Barnett, S. A. 1958. Experiments on 'neophobia' in wild and laboratory rats. *Br. J. Psychol.*, **49**, 195–201.

Barnett, S. A. 1975. *The Rat: A Study in Behavior.* University of Chicago Press: Chicago.

Booth, D. A. 1985. Food-conditioned eating preferences and aversions with interoceptive elements: conditioned appetites and satieties. *Ann. N. Y. Acad. Sci.*, **443**, 22–41.

Galef, B. G., Jr. 1970. Aggression and timidity: responses to novelty in feral Norway rats. *J. comp. physiol. Psychol.*, **70**, 370–381.

Galef, B. G., Jr. 1986. Social interaction modifies learned aversions, sodium appetite, and both palatability and handling-time induced dietary preference in rats (*Rattus norvegicus*). *J. comp. Physiol.*, **100**, 432–439.

Galef, B. G., Jr. 1989a. An adaptationist perspective on social learning, social feeding and social foraging in Norway rats. In: *Contemporary Issues in Comparative Psychology* (Ed. by D. A. Dewsbury), pp. 55–79. Sunderland, Massachusetts: Sinauer.

Galef, B. G., Jr. 1989b. Enduring social enhancement of rats' preferences for the palatable and the piquant. *Appetite*, **13**, 81–92.

Galef, B. G., Jr. 1990. An historical perspective on recent studies of social learning about food by Norway rats. *Can. J. Psychol.*, **44**, 311–329.

Galef, B. G., Jr. 1991. Information centres of Norway rats: sites for information exchange and information parasitism. *Anim. Behav.*, **41**, 295–301.

Galef, B. G., Jr & Kennett, D. J. 1985. Delays after eating: effects on transmission of diet preferences and aversions. *Anim. Learn. Behav.*, **13**, 39–43.

Galef, B. G., Jr, Kennett, D. J. & Wigmore, S. W. 1984. Transfer of information concerning distant foods in rats: a robust phenomenon. *Anim. Learn. Behav.*, **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. *Anim. Behav.*, **31**, 748–758.

Garcia, J. & Koelling, R. A. 1966. Relation of cue to consequence in avoidance learning. *Psychonom. Sci.*, **4**, 123–124.

Meehan, A. P. 1984. *Rats and Mice: Their Biology and Control.* Tonbridge, U.K.: Brown, Knight & Truscott.

Rozin, P. 1976. The selection of foods by rats, humans and other animals. In: *Advances in the Study of Behavior. Vol. 6* (Ed. by J. S. Rosenblatt, R. A. Hinde, E. Shaw & C. Beer), pp. 21–76. New York: Academic Press.

Rzoska, J. 1953. Bait shyness, a study in rat behaviour. *Br. J. Anim. Behav.*, **1**, 128–135.

Shorten, M. 1958. The reaction of the brown rat towards changes in its environment. In: *Control of Rats and Mice. Vol. 2* (Ed. by D. Chitty), pp. 307–334. Oxford: Clarendon Press.

Siegel, S. 1974. Flavor preexposure and 'learned safety'. *J. comp. physiol. Psychol.*, **87**, 1073–1082.

Ward, P. & Zahavi, E. 1973. The importance of certain assemblages of birds as 'information-centres' for food-finding. *Ibis*, **115**, 517–534.

Winocur, G. 1990. Anterograde and retrograde amnesia in rats with dorsal hippocampal or dorsomedial thalmic lesions. *Behav. Brain Res.*, **38**, 145–154.

Young, P. T. 1959. The role of affective processes in learning and motivation. *Psychol. Rev.*, **66**, 104–125.