



Social exploitation of intermittently available foods and the social reinstatement of food preference

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To determine whether Norway rats, *Rattus norvegicus*, could use socially acquired information to track recurrences of an intermittently available food (experiment 1), we allowed observer rats to interact every 2–3 days with demonstrator rats fed one of two diets, then determined the amount of each diet eaten by observers. We found that observer rats showed repeated significant increases in their preferences for foods their respective demonstrators had eaten. Because social interactions repeatedly enhanced preference for a food, we reasoned that after the socially induced food preference of an animal (A1) had waned, that preference might be reinstated in A1 by interaction with a conspecific (A2) in whom A1 had previously induced a preference for the food. In experiment 2, we demonstrated such social reinstatement of a food preference.

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The results of experiments conducted both in our laboratory and elsewhere have shown repeatedly that after a naïve Norway rat, *Rattus norvegicus* (an observer) interacts with a conspecific that has eaten a food (a demonstrator), the observer shows substantial enhancement of its preference for whatever food its demonstrator ate (Galef & Wigmore 1983; Posadas-Andrews & Roper 1983; Heyes & Durlach 1990; Winocur 1990). Similar effects of interaction with conspecific demonstrators on the food preferences of their observers have been reported in species as diverse as red-winged blackbirds, *Agelaius phoeniceus* (Mason & Reidinger 1981) and spotted hyaenas, *Crocuta crocuta* (Yoerg 1991).

Although one animal's influence on the food choices of others is well established and considerable progress has been made in analysing the behavioural processes that support social influences on food preference (for reviews, see Galef 1988, 1996), relatively little is known about how animals might use socially acquired information to increase their foraging efficiency in natural habitats. The lack of control inherent in field situations makes direct investigation of the contribution of socially acquired information to foraging efficiency difficult, if not impossible. However, direct measurement in natural situations is not the only way to investigate the way in which social learning might function to increase foraging efficiency.

In a pair of recent papers (Galef 1993; Galef & Whiskin 1994), we looked for boundary conditions on the social induction of food preferences in Norway rats. We reasoned that any limits on the circumstances permitting social induction of food preference that we discovered could be used to generate hypotheses about how animals might use socially acquired information to facilitate foraging in natural circumstances. For example, we found that social enhancement of food preference was significantly greater if the food eaten by a demonstrator rat was unfamiliar to its observer than if the observer had recently eaten the food the demonstrator ate. On the basis of this finding, we hypothesized that social induction of food preference would tend to broaden the feeding repertoires of rats, motivating them to ingest unfamiliar foods that their fellow colony members were eating (Galef 1993).

We subsequently discovered that the inhibitory effect of familiarity on an observer rat's later susceptibility to social induction of a preference for a food lasts only 1–2 days (Galef & Whiskin 1994). Consequently, we hypothesized that socially acquired information might motivate a Norway rat to seek out and ingest not only totally unfamiliar foods, but also any intermittently available foods that others in its colony had rediscovered (Galef & Whiskin 1994).

The first of the two experiments described here tests this second hypothesis. If, as we proposed (Galef & Whiskin 1994), rats can use socially acquired information to exploit successive reappearances of an intermittently available food, then they should be susceptible to

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repeated social inductions of preference for that food.

EXPERIMENT 1

We undertook experiment 1 to determine whether Norway rats would respond repeatedly to social induction of preference for a food.

Methods

Subjects

Sixteen experimentally naïve, 42-day-old, female Long-Evans rats served as observers. These animals were born in the vivarium of the McMaster University Psychology Department (Hamilton, Ontario) to breeding stock acquired from Charles River Canada (St Constant, Quebec). An additional 16 50-day-old rats that had served as subjects in previous experiments served as demonstrators.

Foods

We made two diets by adding either 1.0 g of bulk-ground cinnamon (diet Cin) or 2.0 g of Hershey's Pure Cocoa (diet Coc) to 100 g of powdered Purina Laboratory Rodent Diet No. 5001 (diet Pur). Pretesting of 10 rats established that diets Cin and Coc were roughly equally palatable (Mean \pm SE percentage of diet Cin eaten by six rats during a 24-h choice between Diets Cin and Coc = $49.5 \pm 5.5\%$).

Apparatus

We housed demonstrator and observer rats separately in temperature- and humidity-controlled colony rooms illuminated on a 12 h light:dark schedule. During the experiment, rats were maintained in individual wire-mesh, hanging cages measuring $18 \times 34 \times 19$ cm. We presented food to both observers and demonstrators in semicircular, stainless steel dishes (10-cm diameter, 4 cm deep), filled to only half their depth to prevent spillage.

Procedure

To begin, we placed all 16 demonstrators on a 23-h food-deprivation schedule that lasted for 13 days. For the first 2 days of scheduled feeding, we fed all demonstrators Diet Pur for 1 h/day. During the next 11 daily 1-h feeding periods, we fed eight of the demonstrators diet Cin and the remaining eight demonstrators diet Coc.

Day 1. The experiment proper began with the third 1-h period of scheduled feeding of demonstrators which was the first day on which we fed each demonstrator either diet Cin or diet Coc. Immediately after this feeding, we placed one demonstrator in the home cage of each observer, and then left demonstrator-observer pairs undisturbed to interact for 30 min. Following this 30-min interaction period, we returned each demonstrator to its

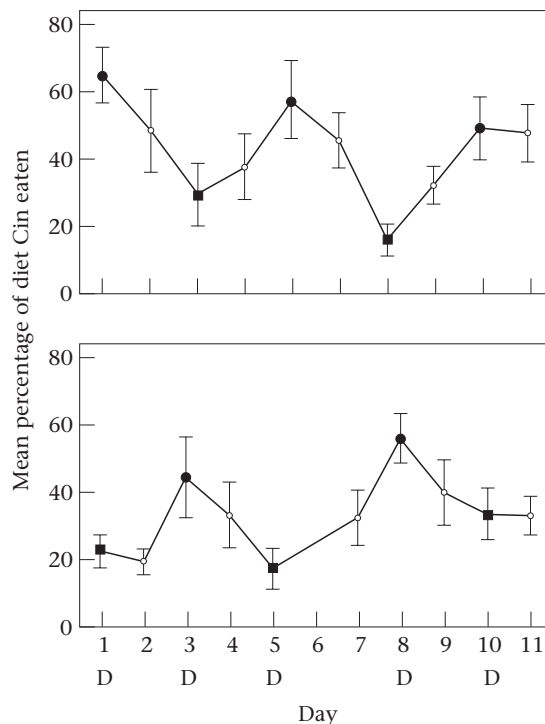


Figure 1. Mean \pm SE percentage of cinnamon-flavoured diet (diet Cin) eaten by observer rats ($N=16$) on days 1–11 of experiment 1 following interaction with a demonstrator fed diet Cin (●) or diet Coc (■). Each observer rat interacted with a demonstrator rat on each day labelled with a D.

home cage and then placed two weighed food dishes, one containing diet Cin and the other diet Coc, in each observer's cage.

Day 2–11. Twenty-three hours later, we removed the food dishes from each observer's cage, weighed them, and 1 h later replaced them in that observer's cage. We continued: (1) to allow demonstrators and observers to interact for 30 min following the daily 1-h feeding schedule for demonstrators on days 3, 5, 8 and 10 (see below); (2) to offer observers a choice between weighed samples of diets Cin and Coc for 23 h/day; and (3) to determine observers' intakes of diets Cin and Coc each day for the remaining 10 days of the experiment.

Figure 1 depicts both the schedule on which observer rats interacted with demonstrators and the food fed to those demonstrators before they interacted with their observers. The eight observer rats that had interacted with a demonstrator fed diet Cin on day 1 of the experiment each interacted with a demonstrator fed diet Cin on days 5 and 10 and with a demonstrator fed diet Coc on days 3 and 8. The eight observer rats that had interacted with a demonstrator fed diet Coc on day 1 of the experiment interacted with a demonstrator fed diet Coc on days 5 and 10 and with a demonstrator fed diet Cin on days 3 and 8. We scheduled interactions of demonstrators and observers so that no observer interacted with the same demonstrator twice.

Data analysis

We used within-subject, nonparametric analyses (sign tests) to examine changes in food preferences of observer rats following interaction with demonstrator rats.

Results and Discussion

As expected, given the results of previous experiments (Galef & Wigmore 1983; Galef 1993; Galef & Whiskin 1994), during the 23 h following the observer rats' first interaction with a demonstrator that had eaten diet Cin, observers ate more diet Cin than during the 23 h following their first interaction with a demonstrator rat fed diet Coc (cf. days 1 and 3 in Fig. 1; sign test: $x=0$, $N=16$, $P<0.001$, for both). Similarly, during the 23 h following their last interaction with a demonstrator rat that had eaten diet Cin, observer rats ate more diet Cin than during the 23 h following their last interaction with a demonstrator rat fed diet Coc (cf. day 10 in Fig. 1; $x=0$, $N=16$, $P<0.001$). Similarly, the results of comparisons of food preferences on days 8 and 10 show that Norway rats will respond repeatedly to social inductions of a food preference by increasing their relative intake of that food ($x<3$, $N=16$, $P<0.002$).

EXPERIMENT 2

The results of experiment 1 are consistent with the view that social interactions can repeatedly result in induction of a food preference in Norway rats. Such repeated inductions of food preference in observer rats might provide a way in which a socially induced food preference could be sustained in a colony of rats for longer than would be expected from consideration of only the longevity of socially induced food preferences in individual rats and the time necessary for all individuals in a colony to experience social induction of a preference. Here we asked whether an observer rat (A1) whose socially induced preference for a food had waned, could be induced to prefer that food again by interaction with a rat (A2) in which A1 had previously induced a preference for the food. If so, then at least in principle, a socially induced preference for food should be sustained longer in a population of rats than expected from determination of the longevity of socially induced food preferences in individuals.

Methods

Subjects

Forty-four experimentally naïve, 42-day-old, female Long-Evans rats acquired from Charles River Canada (St Constant, Quebec) served as observers. We randomly assigned observers to two groups ($N=22$ /group); the treatment for each is described below in Procedure. An additional 22 50–56-day-old females that had participated in other experiments served as demonstrators.

Apparatus and foods

We used the same apparatus and foods in experiment 2 that we had used in experiment 1.

Procedure

Each day of the experiment, the experimenter determined the intake of diet Cin by demonstrators and of diets Cin and Coc by observers. The experimenter also calculated the percentage of each observer's total intake that was diet Cin.

Demonstrators. As in experiment 1, we placed demonstrator rats on a 23-h/day deprivation schedule and fed them diet Pur for 1 h/day for 2 successive days before the start of the experiment proper. On the third day of scheduled feeding (day 1 of the experiment), we fed all 22 demonstrator rats weighed samples of diet Cin for 1 h, then placed one demonstrator rat in the home cage of each naïve observer rat assigned to group 1 for 30 min. Following the 30-min interaction period, we removed demonstrators from the observers' cages and ended the participation of the demonstrators in the experiment.

Observers. We placed all observer rats on a 23-h/day feeding schedule and fed them diet Pur for 1 h/day immediately after we fed demonstrators.

On day 1, after demonstrators had interacted with observers in group 1, we offered observers in group 1 a choice between weighed samples of diets Cin and Coc for 1 h and then placed each of the 22 observers, for 30 min, in the cage of one of the 22 subjects assigned to group 2.

After observers assigned to groups 1 and 2 had interacted for 30 min, we returned observers in group 1 to their respective home cages and then offered observers assigned to group 2, for 1 h, a choice between weighed samples of diets Cin and Coc.

On day 2 of the experiment, we again offered observers in group 1 a choice between weighed samples of diets Cin and Coc for 1 h, placed them in the cages of subjects assigned to group 2 for 30 min, and again offered subjects in group 2 a choice between weighed samples of diets Cin and Coc for 1 h.

On days 3 and 4 of the experiment, we offered each observer assigned to group 1 ad libitum access to weighed samples of both diets Cin and Coc. When rats that have a socially induced preference for one of two equally palatable, equally nutritious diets are offered ad libitum access to those diets, they learn in a day or two that the diets are of equivalent value and come to eat equal amounts of each (Galef & Whiskin 1998). Consequently, it was our expectation that, during this 2-day period, the socially induced preference for diet Cin of observers in group 1 would wane.

On days 3, 4 and 5, we offered subjects assigned to group 2 a choice between weighed samples of diets Cin and Coc, but for only 1 h/day. If rats with a socially induced preference for one of two equally palatable, equally nutritious foods have access to them for only a brief time each day, it takes many days for a socially induced preference for one of those diets to wane (Galef & Whiskin 1998). Consequently, it was our expectation that subjects assigned to group 2 would sustain their socially enhanced preference for diet Cin longer than subjects assigned to group 1.

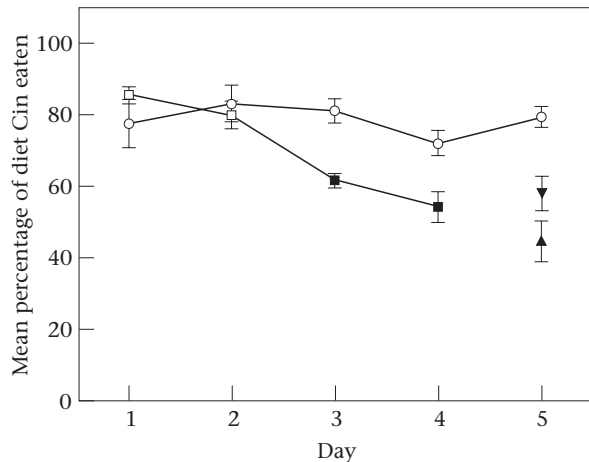


Figure 2. Mean \pm SE percentage of cinnamon-flavoured diet (diet Cin) eaten by subjects assigned to group 2 (○; $N=22$) and observers assigned to group 1: (□: 24-h intake, $N=22$; ■: 1-h intake, $N=22$; and 24-h intake of observers that, on day 5, did (▼, $N=11$) and did not (▲, $N=11$) interact with subjects in group 2 before feeding.

On day 5, at the end of the 1-h feeding period of observers in group 2, we removed the food cups from the cages of observers in group 1, selected those 11 subjects in group 2 that had eaten the greatest proportion of diet Cin during the 1-h feeding period on day 4 and placed those subjects for 30 min in the cages of half of the observers assigned to group 1.

To determine which 11 observers in group 1 should interact with observers in group 2, we first rank-ordered all 22 observers in group 1 in terms of their percentage preference for diet Cin on day 4. We then equated the mean rank order of preference for diet Cin in those observers in group 1 that we would and would not allow to interact with observers in group 2.

After members of group 2 and group 1 had interacted, we removed group 2 members from the group 1 cages, and offered all members of group 1 a choice between diets Cin and Coc for 24 h.

Results and Discussion

As expected, we were successful in inducing a preference for diet Cin in observer rats in group 1. On both days 2 and 3, the percentage of diet Cin eaten by subjects in group 1 was significantly above 49.5+5.5%, (i.e. the percentage of diet Cin eaten by naïve rats offered a choice between diets Cin and Coc for 24 h; see Methods of experiment 1; Fig. 2), and observers in group 2 acquired a preference for diet Cin as a consequence of interacting with observers in group 1. On days 1 and 2, during the 24-h periods following interaction with observers in group 1, observers in group 2 ate 77.5+6.8 and 83.0+3.7% diet Cin, respectively.

Also as expected, observers in group 1, which had ad libitum access to diets Cin and Coc on days 3 and 4, showed a significant decrease in their preference for diet Cin across the first 4 days of the experiment (repeated

measures ANOVA: $F_{3,21}=25.1$, $P<0.0001$), while observers in group 2, which had access to diets Cin and Coc for only 1 h/day, did not show a decrease in their preference for diet Cin across the first 4 days of the experiment (repeated measures ANOVA: $F_{3,21}=1.26$, NS).

Most important, on day 5, observers in group 1 that had interacted with observers in group 2 showed a greater preference for diet Cin than observers in group 1 that had not interacted with observers in group 2 (Mann–Whitney U test: $U=29$, $N_1=N_2=11$, $P<0.05$; Fig. 2, day 5). Thus, observers in group 1 reacquired a tendency to ingest diet Cin as a result of interaction with observers in group 2, whose preference for diet Cin had been induced by interaction with subjects in group 1.

Although the effect of interaction with members of group 2 on the food preferences of members of group 1 on day 5 was small, it resulted from single interactions between one member of group 1 and one member of group 2. In more natural circumstances one might expect repeated interactions between rats to be common. As a result, recursive social effects on food preference might be stronger in natural circumstances than we found them to be in the laboratory (Galef 1989).

GENERAL DISCUSSION

In experiment 1 we determined whether social information concerning reappearance of intermittently available foods could be used by rats to facilitate their exploitation of such foods. Our results were consistent with the hypothesis that socially acquired information allows recipients to exploit reoccurrences of intermittently available foods (Galef 1993). The results of experiment 1 also led us to ask whether reinductions of social preferences in observer rats could increase the longevity of a food preference in a rat population. The results of experiment 2 suggest that the socially induced preference of an animal (A1) for a food can be reinduced after interacting with a conspecific (A2) whose preference for that food had been induced initially by interaction with A1. The results of experiment 2 thus suggest that the process of social reinstatement of preference may maintain socially acquired food preferences in free-living rat populations longer than would be predicted from rates of extinction of a socially induced preference in individual population members. Such recursive social induction is therefore of potential importance in formal models of both social foraging and gene-culture interaction (e.g. Laland et al. 1993, 1996; Giraldeau et al. 1994).

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