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Social influences on the amount of food eaten by Norway rats

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A naive observer Norway rat offered a choice between two foods, after it interacts with a demonstrator rat fed one of those foods, increases its preference for whichever food the demonstrator rat ate. It is not known whether interaction with a demonstrator rat would also increase the amount that an observer rat would eat if it were given access only to the food the demonstrator had eaten. In this study, each observer rat interacted with a demonstrator rat fed a food, either familiar or unfamiliar to the observer, and the observer was then offered a weighed sample of the food that the demonstrator had eaten. It was found that, during the first hour of testing, observer rats that had interacted with demonstrators fed an unfamiliar food, increased their intake of that food roughly four-fold. Observer rats that interacted with demonstrator rats fed a familiar food however, did not increase their food intake. Socially enhanced intake of unfamiliar food was seen only during the first hour that observers had access to food and was compensated for during the next 23 h of feeding. This short-term increase in observer intake of unfamiliar foods appeared to result from socially-induced motivation to ingest unfamiliar foods rather than from socially-induced reduction in neophobia.

Introduction

A naive observer Norway rat (*Rattus norvegicus*) offered a choice between two foods after interacting with a conspecific demonstrator fed one of those foods will increase its relative intake of whichever food its demonstrator ate (Chou & Richerson, 1992; Galef & Wigmore, 1983; Posadas-Andrews & Roper, 1983; Richard, Grover & Davis, 1987; Stetter *et al.*, 1995; Strupp & Levitsky, 1984). Such demonstrator influence on observers' food selections is surprisingly robust (Galef, Kennett & Wigmore, 1985) and can reverse not only palatability-based food preferences (Galef, 1986, 1989; Galef & Whiskin, 1998), but also food preferences resulting from learned aversions or sodium appetites (Galef, 1986, Heyes & Durlach, 1990).

In examining the causes and functions of such social effects on the feeding behavior of rodents, investigators have consistently measured changes in the food preferences of observers offered a choice between foods; social influences on intake of a single food have not been examined. As a consequence, it is not known whether social interactions that alter rats' food preferences also alter their food intake.

The present experiments were undertaken to determine whether interaction with a demonstrator rat fed a distinctively flavored food would increase conspecific observers' intake of that food. Because it has been found previously that diet novelty is an important determinant of expression of social influence on food choice (Galef, 1993; Galef & Whiskin, 1994), in Experiment 1, we looked for effects on observers' intake of interaction with demonstrators fed diets either slightly or totally unfamiliar to their respective observers.

Experiment I

This experiment was conducted to determine whether interaction with a demonstrator rat that had eaten either a relatively familiar or a relatively unfamiliar food would increase its observer's subsequent absolute intake of that food.

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Method

Subjects

Sixty experimentally naive, 48-day-old, female, Long-Evans rats obtained from Charles River Canada (St Constant, Quebec) served as observers. An additional 40, 56- to 62-day-old female rats that had served as observers in previous experiments served here as demonstrators.

Subjects were maintained in a single colony room illuminated on a 12 : 12-h light/dark schedule with light onset at 0800h.They had *ad libitum* access to Purina Rodent Laboratory Chow 5001 for at least 7 days before the start of the experiment.

Apparatus

Throughout the experiment, each of the 100 subjects resided in a stainless-steel hanging cage measuring 20 cm × 20 cm × 34 cm. Food was provided in semi-circular, stainless-steel cups (10 cm in diameter and 5 cm deep) filled to only half their depth to prevent spilling.

As described below, some subjects serving as observers were exposed to glass jars (7 cm high × 5·7 cm diameter) with metal screw tops in each of which a hole 3·2 cm in diameter had been cut. This hole was covered with a piece of hardware cloth (0·64-cm grid) allowing subjects to smell and see the food in a jar, but not to taste it. Each jar was filled with food to within 2 cm of its lid.

Diets

Four different diets were used in the experiment: (1) unadulterated, powdered Purina Rodent Laboratory Chow 5001 (Diet Chow; Ralston-Purina Canada, Woodbridge, Ontario); (2) Diet Chow to which 10 g/kg Club House Pure Ground Cinnamon was added (Diet Cin-Chow); (3) Teklad Normal Protein Test Diet (Diet NPT: Teklad Diets, Madison, WI; Catalogue No. TD 170590; in g/kg: 598·2 corn starch, 260·1 casein, 108·1; 80·0 vegetable oil, 40·0, mineral mix; 20·0 cod-liver oil, and 1·8 vitamin mix); and (4) Diet NPT to which 10 g/kg cinnamon (Diet Cin-NPT) was added.

Procedure

The procedure was the same as that used in our previous studies of social influence on food choice (for a review; see Galef, 1988) except that here, during testing for social influence on ingestion (Step 3), each observer was offered a single food to eat rather than two foods to choose between.

Step 1 All 40 demonstrators were placed on a 23-h schedule of food deprivation, and for 1 h on each of 3 consecutive days, equal numbers of demonstrators were given a weighed food cup containing either Diet NPT, Diet Cin-NPT, Diet Chow, or Diet Cin-Chow. At the end of the last of these 1-h feeding periods, each demonstrator's food cup was weighed and the amount that it had eaten was ascertained.

Step 2 Immediately after demonstrators had finished their third scheduled feeding, one demonstrator was placed in the cage of each of 40 observers and a jar filled with either Diet Cin-NPT or Diet Cin-Chow was placed in the cage of each of the remaining 20 observers. Each observer was then left free to interact with its demonstrator or jar for 30 min, before the jar or demonstrator was removed from each observer's cage.

Step 3 A weighed food cup containing Diet Cin-NPT was placed in the cages of observers that had interacted during Step 2 with: (1) a jar containing Diet Cin-NPT; (2) a demonstrator fed Diet Chow; or (3) a demonstrator fed Diet Cin-NPT. At the same time, a weighed food cup containing Diet Cin-Chow was placed in the cages of observers that had interacted with: (1) a jar containing Diet Cin-Chow; (2) a demonstrator fed Diet Cin-Chow; or (3) a demonstrator fed Diet NPT.

Step 4 An experimenter weighed the food cup in each observer's cage 1, 3, 5, 10, and 24 h after it had been placed there.

Results

Demonstrators ate a mean (± 1 *SEM*) of $6{\cdot}2 \pm 0{\cdot}3$ g during the hour before they interacted with their respective observers (Step 2), and there was no difference in the amount eaten by demonstrators fed Diet Cin-Chow and Diet Cin-NPT ($F(3, 37) = 1{\cdot}41$, *NS*).

Data were lost from one observer that urinated in her food cup and from two observers when, because of clogged water bottles, their demonstrators failed to eat on Day 3 of Step 1.

The main results of Experiment 1 are presented in Fig. 1a and b. The figure shows the mean g/h eaten by observers offered the relatively unfamiliar Diet Cin-NPT (Fig. 1a) and the relatively familiar Purina chow-based Diet Cin-Chow (Fig. 1b) during testing (Step 3).

As can be seen in the upper panel of Fig. 1, treatment of demonstrators had a profound influence on their observers' intake of the relatively unfamiliar Diet Cin-NPT (Repeated-measures ANOVA, $F(2, 25) = 12{\cdot}89$, $p < 0{\cdot}0001$). Further, there was a significant hour of testing × group interaction ($F(4, 50) = 12{\cdot}82$, $p < 0{\cdot}0001$). These effects reflected greater intake of Diet Cin-NPT during the first hour of testing by observers that interacted with demonstrators fed Diet Cin-NPT.

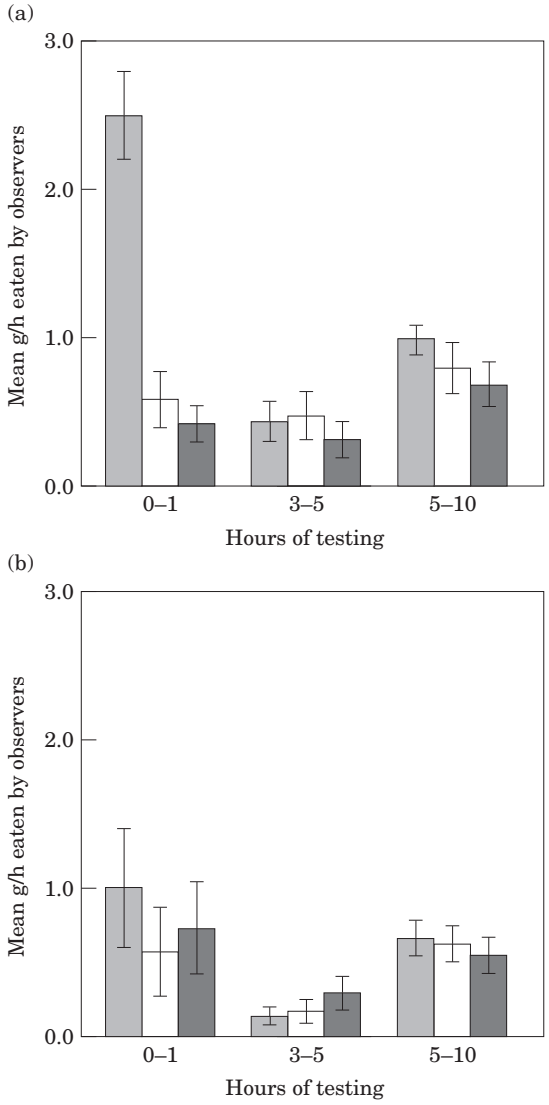

Figure 1. (a) Mean grams of Diet Cin-NPT eaten per hour by observer rats that interacted during Step 2 with either a jar containing Diet Cin-NPT, or demonstrator rats fed either Diet Cin-NPT or Diet Chow. (b) Mean grams of Diet Cin-Chow eaten per hour by observer rats that had interacted with either a jar containing Diet Cin-Chow or demonstrator rats fed either Diet Cin-Chow or Diet NPT. Flags = ±1 *SEM*. ▒, Diet Cin-NPT demonstrator; ■, Diet Chow demonstrator; ▒, Diet Cin-NPT Jar.

Neither interaction with a demonstrator fed Diet Chow (controlling for effects of social interaction *per se*) nor interaction with a jar containing Diet Cin-NPT (controlling for effects of simple exposure to Diet Cin-NPT) affected observers' intake of Diet Cin-NPT (Tukey-Cramer Multiple Comparisons Test, Diet Cin-NPT Group greater than both Cin-NPT Jar Group and Diet Chow Group, both qs $> 8{\cdot}65$, both ps $< 0{\cdot}001$).

As can be seen in the lower panel of Fig. 1, there was no effect of treatment of demonstrators on the amount of the relatively familiar Diet Cin-Chow that observers ate during testing (Repeated-measures ANOVA, $F(2, 26) = 0{\cdot}33$, *NS*). There was also no significant hour × group interaction ($F(4, 52) = 0{\cdot}81$, *NS*).

Comparison of the ingestive behavior during the first hour of testing of observers eating Diet Cin-NPT and Diet Cin-Chow revealed a highly significant main effect of both group ($F(2, 55) = 17{\cdot}39$, $p < 0{\cdot}0001$) and diet ($F(1, 55) = 5{\cdot}80$, $p < 0{\cdot}02$). There was also a significant interaction between group and diet eaten during testing (Between-subjects ANOVA; $F(2, 55) = 5{\cdot}74$, $p < 0{\cdot}005$) again reflecting the impact of interaction of observers fed Diet Cin-NPT with demonstrators fed Diet Cin-NPT.

There was no difference in the total amount eaten during the entire 24 h of testing either by observers in the three groups fed Diet Cin-NPT ($F(2, 27) = 0{\cdot}57$, *NS*) or by observers in the three groups fed Diet Cin-Chow ($F(2, 28) = 0{\cdot}70$, *NS*).

Discussion

The results of Experiment 1 indicate that interaction with a demonstrator rat fed an unfamiliar diet (Diet Cin-NPT) increased observers' intake of that diet the first time that observers encountered it. To the contrary, interaction with a demonstrator fed a relatively familiar diet (Diet Cin-Chow) did not increase observers' intake of that diet.

The finding that social influence on ingestion may be more powerful when foods are unfamiliar than when they are familiar is consistent with results of previous experiments. For example, Forkman (1991) has reported that satiated Mongolian gerbils paired with a hungry conspecific eating either a familiar or unfamiliar food will eat more of the unfamiliar, but not of the familiar food. In a similar fashion, we have reported that observer rats exhibit greater social enhancement of their preferences for unfamiliar than for familiar foods (Galef, 1993; Galef & Whiskin, 1994). Such findings, like those in the present experiment, suggest that rodents use social information when selecting foods to incorporate into their feeding repertoires (Forkman, 1991; Galef & Whiskin, 1994; Murton, 1971).

Although both suggestive and consistent with previous findings, the results of Experiment 1 do not provide unequivocal evidence that differences in diet familiarity were responsible for the different outcomes seen in the left and right panels of Fig. 1. Socially acquired information concerning Diet Cin-Chow might simply not have been as effective in changing food intake of observer rats as was socially acquired information concerning Diet Cin NPT.

Experiment 2

Experiment 2 was undertaken to examine directly the role of diet familiarity in mediating social influence on food intake.

Method

Subjects

Forty, experimentally naive, 40-day-old, female Long-Evans rats, randomly assigned to four conditions served as observers, and 40, 56-day-old female Long-Evans rats that had served as observers in previous experiments served here as demonstrators.

Apparatus and diets

The apparatus and diets were those used in Experiment 1.

Procedure

The procedure of Experiment 2 was similar to that of Experiment 1, except that here: (1) for 3 days before observers interacted with their respective demonstrators (Step 2), 20 observers were given *ad libitum* access to Diet Cin-NPT and 20 observers were given *ad libitum* access to Diet Chow; (2) during Step 2, half the observers that had eaten Diet Cin-NPT and half those that had eaten Diet Chow interacted with demonstrators fed Diet Cin-NPT and the rest with demonstrators fed Diet Chow; and (3) all 40 observers were offered Diet Cin-NPT during testing (Step 3).

Because in Experiment 1 observers' intake of Diet Cin-NPT was affected by interaction with demonstrators fed Diet Cin-NPT only during the first hour of testing, in Experiment 2 observers' intake was measured only during that hour.

Results and discussion

The main results of Experiment 2 are presented in Fig. 2 which shows the mean amount of Diet Cin-NPT eaten during testing by observers assigned to the various groups. As visual inspection of Fig. 2 reveals, there was a main effect on observers' intake of Diet Cin-NPT of both pre-exposure condition ($F(1, 36) = 13{\cdot}65$, $p < 0{\cdot}001$) and diet fed to demonstrators ($F(1, 36) = 4{\cdot}59$, $p < 0{\cdot}04$). There was also a significant interaction between these main effects ($F(1, 36) = 4{\cdot}58$, $p < 0{\cdot}04$). As in social influence on rats' food preferences (Galef, 1993; Galef & Whiskin, 1994), social influence on rats' food intake is greater if the food about which social information has been acquired is unfamiliar than if it is familiar.

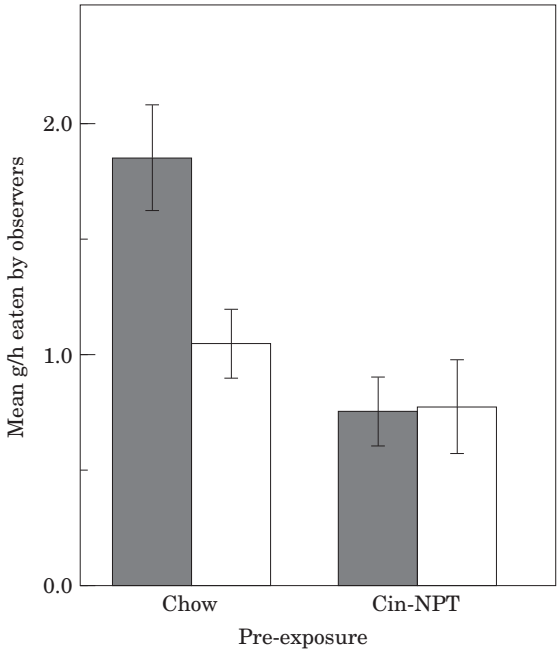

Figure 2. Mean grams of Diet Cin-NPT eaten during the first hour of testing by observer rats pre-exposed for 3 days to either Diet Cin-NPT or Diet Chow. Flags = ±1 *SEM*. ■, Diet Cin-NPT demonstrator; ■, Diet Chow demonstrator.

Experiment 3

Experiment 3 was undertaken to determine for how long after observer rats interacted with conspecific demonstrators fed an unfamiliar diet, the observers would continue to exhibit enhanced intake of the food that their demonstrators had eaten.

Method

Subjects

Fifty-eight experimentally naive, 48-day-old, female, Long-Evans rats obtained from Charles River Canada (St Constant, Quebec) served as observers. Fifty-eight, 56- to 62-day-old female rats that had served here as observers in previous experiments served here as demonstrators.

Apparatus and diets

The apparatus and diets used in Experiment 3 were those used in Experiments 1 and 2.

Procedure

The procedure of Experiment 3 was identical to that of Experiment 1 except that: (1) during Step 2, half of the

58 observers interacted with a demonstrator fed Diet Cin-NPT and half interacted with a demonstrator fed Diet Chow; (2) different groups of observers, each containing 9 or 10 subjects, were tested for their intake of Diet Cin-NPT either immediately (0-Delay Group), 3 days (3-Day Delay Group) or 7 days (7-Day Delay Group) after they had interacted with their respective demonstrators. During the interval between interaction of observers with their demonstrators (Step 2) and testing of observers assigned to 3-Day Delay and 7-Day Delay Groups, each observer was maintained in its hanging cage and given *ad libitum* access to Diet Chow. (3) intake of each observer was examined for only the first hour of testing (Step 3).

Results and discussion

The main results of Experiment 3 are presented in Fig. 3 which shows the mean amount of Diet Cin-NPT eaten during the first hour of testing by observers assigned to 0-Day, 3-Day, and 7-Day Delay Groups. A 2 (diets fed to demonstrators) $\times$ 3 (delay to testing) ANOVA showed what visual inspection of Fig. 3 suggests. During testing, there was a significant main effect on observers' intakes of Diet Cin-NPT of diet fed to demonstrators ($F(1,46) = 13{\cdot}36$, $p < 0{\cdot}001$). However, neither the effect of delay till testing ($F(2,46) = 0{\cdot}47$, *NS*) nor of the interaction between the two main variables ($F(2,46) = 0{\cdot}41$, *NS*) was statistically significant.

The results of Experiment 3 are consistent with those of Experiments 1 and 2 in indicating that exposure of an observer rat to a conspecific demonstrator that has eaten an unfamiliar food affects the amount of that food that the observer eats during the first hour that it has access to it. The result of Experiment 3 show further that effects of interaction with a demonstrator persevere for at least 1 week following interaction between demonstrator and observer.

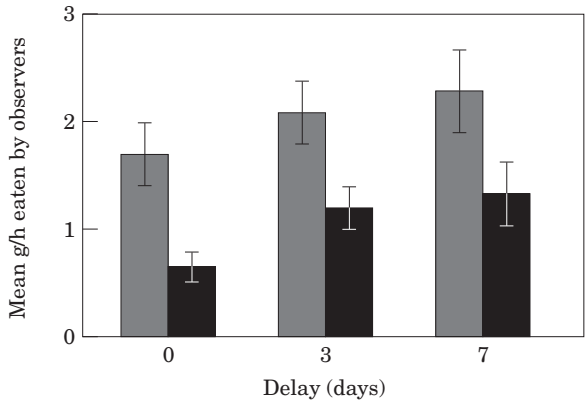

Figure 3. Mean grams of Diet Cin-NPT eaten by observer rats during the first hr of testing that took place either immediately, 3 days, or 7 days after interacting with demonstrators fed either Diet Cin-NPT or Diet Chow. Flags = ± 1 *SEM*. ■, Diet Cin-NPT demonstrator; ■, Diet Chow demonstrator.

General discussion

The results of the present experiments extend previous demonstrations of social influence on rats' feeding behavior by providing evidence that social interaction can affect food intake as well as food choice. However, effects of social influence on food intake, unlike those on food choice (Galef, 1986) were relatively transitory, increasing intake during only the first hour of food availability, and having no effect on intake over 24 h.

Social influence on intake, like social influence on preference, was markedly affected by diet familiarity, with observers exhibiting socially enhanced intake only of relatively unfamiliar foods. It might be argued that in the present experiments social interaction acted to overcome a hesitancy of observers to ingest an unfamiliar food. However, this is probably not the case. As can be seen in Fig. 1, observers that interacted with demonstrators fed Diet Chow ate as much Diet Cin-NPT as Diet Cin-Chow during the first hour of testing. The effect of socially acquired information on intake appears to have been to motivate enhanced ingestion of an otherwise acceptable food (Galef, Whiskin & Bielavska, 1997), rather than to overcome resistance to eating an unfamiliar food.

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