Anim. Behav., 1998, **55,** 967–975

Determinants of the longevity of socially learned food preferences of Norway rats

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(Received 2 January 1997; initial acceptance 18 March 1997; final acceptance 2 July 1997; MS. number: A7806R)

Abstract. We conducted three experiments to examine variables that might influence the longevity of socially induced food preferences in Norway rats. The duration of social influence on the food choices of 42-day-old rats (1) increased with both increasing numbers of demonstrators and increasing numbers of demonstrations by a single demonstrator, (2) varied with the temporal distribution of demonstrations, but (3) did not vary with the age of demonstrators. The results suggest that a single episode of social learning produces short-term, but not long-term, effects on a Norway rat's food choices.

The question of how long socially learned behaviours can persist when they produce no greater (or lesser) reward than alternative courses of action has engendered some discussion (Heyes 1994; Galef 1996; Laland 1996). Such discussion is likely to be prolonged because essentially nothing is known about factors that affect the persistence of socially learned behaviours when they and their alternatives are approximate functional equivalents.

In the present series of experiments, we used social learning of food preferences in Norway rats (reviewed in Galef 1988) as a model system in which to explore factors that might affect the longevity of arbitrary, socially transmitted behaviours. Such variables are biologically important because they could determine whether a socially learned behaviour would be likely to spread through a population and how long it might be expected to persist in individuals.

EXPERIMENT 1: NUMBER OF DEMONSTRATORS

Galef and his coworkers have repeatedly found that interaction of a young rat (an observer rat) with a slightly older conspecific that had eaten a distinctively flavoured food (a demonstrator rat) substantially enhances the observer rat's subsequent preference for whatever food its demonstrator ate (reviewed in Galef 1988, 1996).

Comparisons across past experiments suggest that socially induced food preferences in rats are relatively transient if each observer interacts with a demonstrator on only one occasion (e.g. Galef & Wigmore 1983), but may last longer when an observer experiences several similar demonstrations (e.g. Galef 1989). In experiment 1, we directly examined effects of the number of demonstrator rats with which an observer rat interacted on the longevity of socially induced changes in the observer's food preferences.

Methods

Subjects

Forty-eight, 42-day-old, experimentally naive, female Long-Evans rats served as observers. The rats were born in the vivarium of the Psychology Department of McMaster University (Hamilton, Ontario) to breeding stock that we acquired from Charles River Canada (St. Constant, Quebec).

From weaning (on day 21 postpartum) to the start of the experiment on day 42 postpartum, we housed observer rats in shoebox cages in same-sex groups of three or four siblings. They received ad libitum access to pellets of Purina Rodent Laboratory Chow 5001 (Ralston-Purina Canada, Woodbridge, Ontario) and water.

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We used as demonstrators an additional 48 female Long-Evans rats, 50–60 days old, that had served as observers in other experiments. Before beginning, we randomly assigned 16 observers and 16 demonstrators to each of one-demonstrator, three-demonstrator and five-demonstrator conditions.

Apparatus

We housed observer rats in individual wire-mesh hanging cages (21.5 × 24 × 27.5 cm). Demonstrator rats were housed in cages identical to those of observers and placed in a room separate from them. We presented food to all subjects in semicircular, stainless steel cups (8 cm diameter, 4 cm deep). To prevent spillage, we filled food cups to a depth of 2 cm or less.

Food

We composed two distinctively flavoured diets by adding either 2.0 g of Hershey's Pure Cocoa (diet Coc) or 1.0 g of bulk ground cinnamon (diet Cin) to 100 g of powdered Purina Rodent Laboratory Chow 5001 (diet Pur).

Procedure

Demonstrators. We introduced demonstrator rats into their individual cages and placed them on a 23-h schedule of food deprivation. While on schedule, demonstrator rats had access to diet Pur for 1 h/day for 2 consecutive days.

Twenty-three hours after each demonstrator's second scheduled feeding with diet Pur, we introduced a weighed food cup containing diet Cin into the home cages of 24 demonstrators and a weighed food cup containing diet Coc into the home cages of the remaining 24 demonstrators. One hour later, we removed the food cups from each demonstrator rat's cage, then introduced her into the home cage of an observer rat. We left each demonstrator rat undisturbed for 30 min to interact with its observer. At the end of the 30-min period of interaction between demonstrator and observer, we returned each demonstrator to her home cage. At this point, we ended participation in the experiment of the eight demonstrator rats fed diet Cin and eight demonstrator rats fed diet Coc that we had assigned to the one-demonstrator condition.

The eight demonstrators fed diet Cin and eight demonstrators fed diet Coc that had interacted with observers assigned to the three-demonstrator condition remained on a 23 h/day deprivation schedule for 2 additional days. On each of these 2 days, each demonstrator ate, for 1 h, the same diet that it had eaten on the third day of scheduled feeding. Immediately after eating, each demonstrator interacted, for 30 min, with a different observer rat than on the preceding day. After each demonstrator assigned to interact with an observer assigned to the three-demonstrator condition had interacted with its third observer, we removed her from the experiment.

The remaining eight demonstrators fed diet Cin and eight demonstrators fed diet Coc interacted with the 16 observers assigned to the five-demonstrator condition. Each of these demonstrators remained on a 23 h/day deprivation schedule, ate either diet Cin or diet Coc for 1 h/day, and interacted for 30 min on each of 5 successive days with five different observer rats that we had assigned to the five-demonstrator condition.

Observers. During the first 2 days of the experiment (while we habituated demonstrators to their feeding schedule), we provided each observer rat with ad libitum access to pellets of diet Pur. We removed these pellets just before we introduced a demonstrator into each observer's cage for the first time.

Each observer assigned to the one-demonstrator condition interacted with a single demonstrator rat fed either diet Cin or diet Coc. Each observer assigned to the three-demonstrator condition interacted on 3 successive days with either three different demonstrator rats fed diet Cin or three different demonstrator fed diet Coc. Each observer assigned to the five-demonstrator condition interacted on 5 successive days with either five different demonstrators fed diet Cin or five different demonstrators fed diet Coc immediately before they interacted with their respective observers.

On each day of the experiment, immediately after we removed each demonstrator from its observer's cage, we offered the observer a choice between weighed samples of diet Cin and diet Coc for 23.5 h. We removed food cups from the cage of each observer assigned to the three- and five-demonstrator conditions just before we introduced a demonstrator into that observer's cage.

After each observer rat had finished interacting with the appropriate number of demonstrators, we continued to offer her a choice between diet Cin and diet Coc for 23.5 h/day for 9 successive days.

The experimenter (1) ensured that during the hour before demonstrators interacted with observers, each demonstrator had eaten at least 2 g of diet, (2) weighed both food cups from each observer's cage on each day of the experiment and (3) calculated the percentage of each observer's total daily intake that was diet Cin.

Data Analysis. To evaluate the difference in longevity of any socially induced alterations in food choices of observer rats assigned to one-, three- and five-demonstrator conditions, for each of the 9 days following the last interaction of each observer rat with a demonstrator rat, we compared the food choices of observer rats in each condition that interacted with demonstrator rats fed diet Cin with those of observer rats that interacted with demonstrator rats fed diet Coc. We first established the median percentage of diet Cin eaten on each of the last 9 days of the experiment by observer rats in one-, three- and five-demonstrator conditions that had interacted with demonstrator rats fed diet Coc. We then compared the percentage of diet Cin eaten on each day by each observer rat that had interacted with a demonstrator fed diet Cin with the median percentage of diet Cin eaten on that day by observer rats that had interacted with demonstrator rats fed diet Coc. Next, we counted the number of days on which each observer that interacted with demonstrators fed diet Cin ate a greater percentage of diet Cin than the median percentage of diet Cin eaten by observers in the same condition that interacted with demonstrators fed diet Coc. Last, we performed a one-way ANOVA on the number of days on which each observer rat that had interacted with a demonstrator fed diet Cin ate a greater percentage of diet Cin than the median percentage of diet Cin eaten by observer rats assigned to the same condition that had interacted with a demonstator rat fed diet Coc.

Results and Discussion

The longevity of the socially learned food preferences of observer rats was significantly affected by the number of demonstrators with which they interacted ($F_{2,21} = 4.27$, $P < 0.03$; Fig. 1). Observer rats that interacted with three demonstrators showed longer lasting social effects on their food preferences than did observer rats that interacted with a single demonstrator, and observers that interacted with five demonstrators showed longer-lasting social effects on their food choices than did observers that interacted with three demonstrators, although only the difference in longevity of socially learned food choices of observers assigned

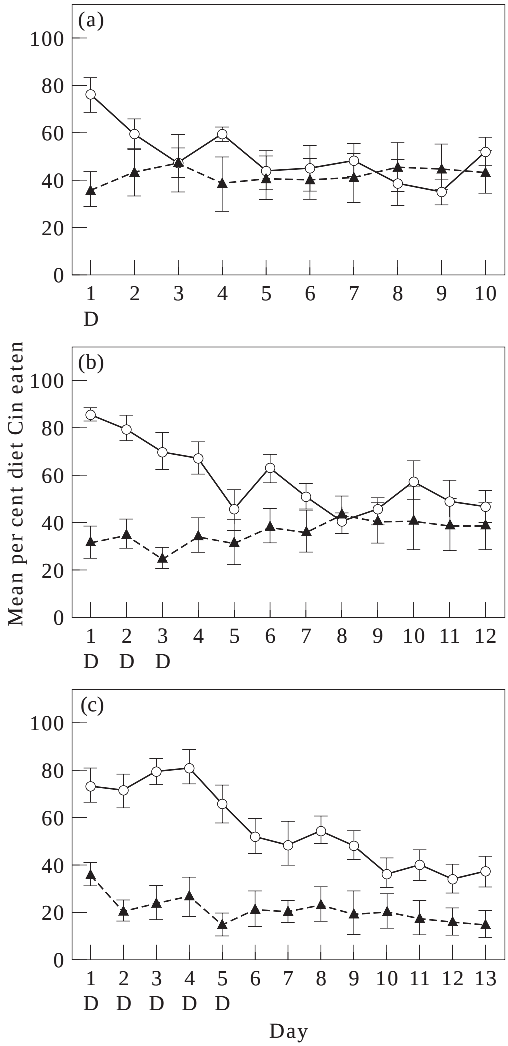

Figure 1. Amount of cinnamon-flavoured diet (diet Cin) eaten, as a percentage of total intake, by observer rats that interacted with (a) one, (b) three or (c) five demonstrator rats fed either diet Cin (○) or diet Coc (▲). Days marked with a D are those on which demonstrators and their observers interacted.

to one- and five-demonstrator conditions was statistically reliable (Tukey–Kramer multiple comparisons test, $q=4.1$, $P<0.05$).

The finding that the duration of a socially enhanced food choice increases with increasing numbers of interactions with demonstrators that have eaten a food is consistent with reports (1) of induction of food preferences of greater magnitude following interaction with two rather than one demonstrator rat (Galef 1986, experiment 1) and (2) of a positive frequency-dependent bias in the food choices of Norway rats exposed to several demonstrator rats, some of which had eaten each of the two diets that observer rats subsequently chose between (Chou & Richerson 1992; Galef et al. 1990a).

EXPERIMENT 2: NUMBER OF DEMONSTRATIONS AND AGE OF DEMONSTRATORS

In experiment 1, observers assigned to one-, three- and five-demonstrator conditions interacted with different numbers of demonstrators fed either diet Cin or diet Coc and, consequently, received different numbers of demonstrations of diet Cin or diet Coc. In experiment 2, we varied the number of demonstrations that each observer experienced while holding constant, at one, the number of demonstrators with which each observer interacted.

Comparing the results of experiment 2 to those of experiment 1 allowed us to determine whether differences in the number of demonstrators or the number of demonstrations were responsible for differences in the longevity of socially learned food preferences shown by observers assigned to one-, three- and five-demonstrator conditions in experiment 1.

At the same time that we explored the effect of number of demonstrations on the longevity of socially learned food preferences of observer rats, we also looked for effects of age of demonstrator rats on the longevity of a socially learned food preference. One might expect effects of interaction with adult demonstrator rats on observers' food choices to be longer lasting than those of interaction with juvenile demonstrator rats. By surviving to adulthood, an adult rat demonstrates the adequacy of its dietary repertoire; a juvenile rat may not have developed comparable competence in diet selection. Consequently, fidelity to diet choices induced by interaction with juveniles should incur greater risk than fidelity to diet choices induced by interaction with adults.

On the other hand, results of an earlier experiment in our laboratory failed to provide evidence of an effect of age of demonstrator rats on the magnitude (rather than the longevity) of social influences on the food choices of observer rats (Galef et al. 1984). Consequently, despite theoretical justification for looking for effects of demonstrator age on longevity of a socially induced food preference, we were not confident of a positive outcome.

Methods

Subjects

Sixty-four experimentally naive, 42-day-old female Long-Evans rats from the vivarium of the McMaster University Psychology Department served as observers in experiment 2.

An additional 28, 50- to 60-day-old rats and 36 150- to 180-day-old rats that had participated in other experiments served, respectively, as juvenile and adult demonstrator rats.

Apparatus and Diets

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

Procedure

The procedure of experiment 2 was the same as that used with subjects assigned to the one-demonstrator and five-demonstrator conditions of experiment 1 except that in experiment 2, each observer rat interacted with only one demonstrator rat; that is (1) seven observer rats interacted with a demonstrator rat, 50–60 days old, fed diet Cin, (2) seven observer rats interacted with a demonstrator rat, 50–60 days old, fed diet Coc, (3) nine observer rats interacted with a demonstrator rat, 150–180 days old, fed diet Cin, and (4) nine observer rats interacted with a demonstrator rat, 150–180 days old, fed diet Coc.

Other observer rats interacted with the same demonstrator rat on 5 successive days: (1) six observer rats interacted with a demonstrator rat, 50–60 days old, fed diet Cin, (2) six observer rats interacted with a demonstrator rat, 50–60 days

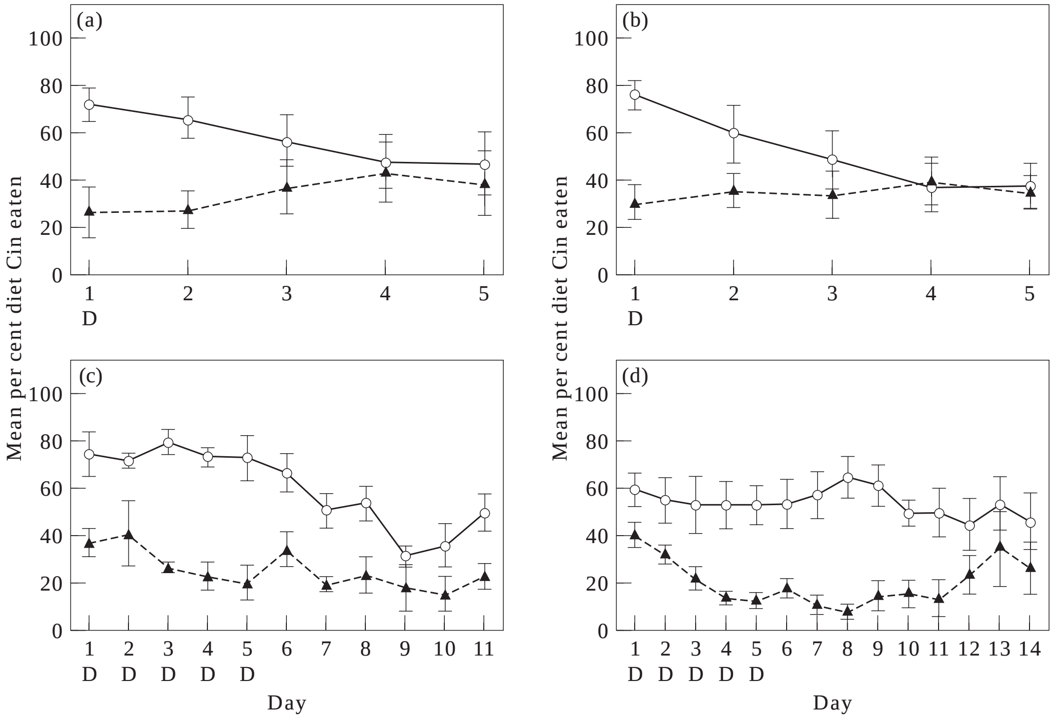

Figure 2. Amount of cinnamon-flavoured diet (diet Cin) eaten, as a percentage of total intake, by observer rats that interacted (a) once with a demonstrator rat, 50–60 days old, (b) once with a demonstrator rat, 150–180 days old, (c) five times with a demonstrator rat 50–60 days old or (d) five times with a demonstrator rat 150–180 days old fed diet Cin (○) or diet Coc (▲). Days marked with a D are those on which demonstrators and their observers interacted.

old, fed diet Coc, (3) 10 observer rats interacted with a demonstrator rat, 150–180 days old, fed diet Cin, and (4) 10 observer rats interacted with a demonstrator rat, 150–180 days old, fed diet Coc.

Data Analysis. We analysed the results of experiment 2 as we had done in experiment 1, except that we used Student's *t*-tests rather than ANOVA to determine levels of statistical significance.

Results and Discussion

Effects of number of demonstrations

Observer rats that interacted five times with one demonstrator (Fig. 2c, d) showed longer-lasting preferences for the foods eaten by their respective demonstrators than did observer rats that interacted only once with a demonstrator (observers interacting with juvenile demonstrators: $t_{12}=5.68$, $P<0.01$; Fig. 2a, c; observers interacting with adult demonstrators: $t_{18}=2.93$, $P<0.01$; Fig. 2b, d).

Comparison of the food choices of observer rats that interacted with five different juvenile demonstrators in experiment 1 with those of observers receiving five demonstrations from a single juvenile demonstrator in experiment 2 revealed that the longevity of the food preference induced by interaction with five different demonstrators (Fig. 1c) did not differ from that induced by five demonstrations by a single demonstrator ($t_{12}=0.31$, NS; Fig. 2c).

Thus, the number of demonstrations, rather than the number of demonstrators, affects the longevity of a socially induced food preference. If interaction with several different individuals that had each eaten the same unfamiliar food were needed to increase the longevity of a socially induced food choice in an observer rat, then it would be relatively difficult for the habit of eating a new food to spread through a colony of rats as the result of social learning. Only after a number of rats had learned individually to eat the same food could social induction of a relatively stable

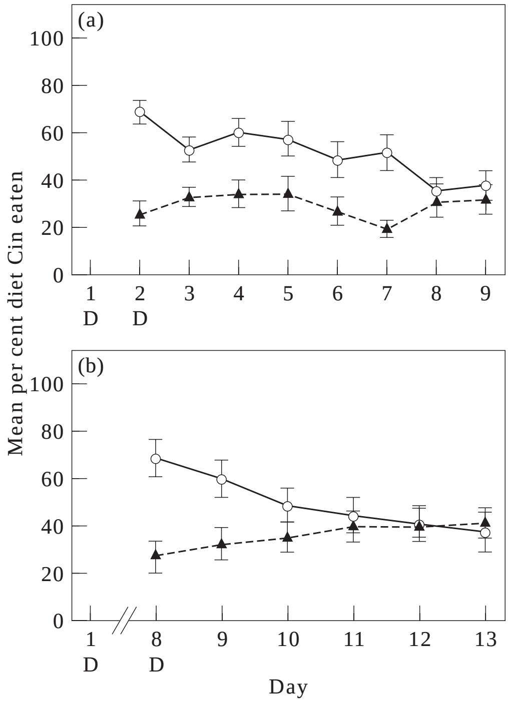

Figure 3. Amount of cinnamon-flavoured diet (diet Cin) eaten, as a percentage of total intake, by observer rats that interacted either (a) on 2 successive days or (b) on 2 days separated by 7 days with a demonstrator rat fed either diet Cin (○) or diet Coc (▲). Days marked with a D are those on which demonstrators and their observers interacted.

food preference for that food occur. If, to the contrary and as the present results suggest, interacting several times with a single individual that had eaten an unfamiliar food induces a relatively stable preference for that food, then social interaction would be more likely to support both the initiation and maintenance of a tradition of food preference in a population of rats.

Effects of age of demonstrators

The age of demonstrator rats did not affect the longevity of food preferences induced in 42-day-old observer rats. The longevity of a socially induced food preference induced either by a single interaction with a demonstrator rat (t_{14}=1.58, NS; Fig. 2a, b) or by five interactions with a demonstrator rat (t_{30}=0.98, NS; Fig. 2c, d) did not vary with demonstrator age. These results suggest that food preferences transmitted vertically (across generations, within a family), obliquely (across generations, but outside family lines) and horizontally (within a generation; Cavalli-Sforza & Feldman 1981; Boyd & Richerson 1985) should have equal longevity.

Our failure to find effects of demonstrator age on the longevity of socially induced food preferences in observer rats suggests that rat age may be added to a growing list of attributes of demonstrators (for example, health, consciousness, familiarity, sex) that might be expected to influence their effectiveness in inducing food preference, but do not (Galef et al. 1983, 1984, 1990b; Horn 1996).

Possible confounds

In the present experiment, as in experiment 1, the number of demonstrations and the number of demonstrators were confounded with duration of demonstration. It is therefore possible that manipulations of both of the number of demonstrations and the number of demonstrators are effective because they alter the time that observer rats interact with demonstrators. Duration of demonstration has been shown to influence the magnitude of the effect of interaction with a demonstrator on the diet choices of its observer (Galef & Stein 1985).

EXPERIMENT 3: TEMPORAL DISTRIBUTION OF DEMONSTRATIONS

In experiment 3, we tested whether the temporal distribution of interactions between demonstrator rats and their observers affected longevity of the observers' socially acquired food choices.

Methods

We conducted experiment 3 as two separate studies. In study 1, we compared the longevity of socially induced diet choices of observer rats that had experienced two demonstrations on the same day and observer rats that had experienced two demonstrations on successive days. In study 2, we compared the effects on the food preferences of observer rats of two demonstrations experienced either 24 h or 7 days apart.

Subjects

Study 1. Forty-two experimentally naive, 42-day-old female Long-Evans rats from the vivarium of the McMaster University Psychology Department served as observers. An additional 42 rats, 50–60 days old, that had participated in other experiments served as demonstrators.

Study 2. Fifty-six experimentally naive, 42-day-old female Long-Evans rats from the vivarium of the McMaster University Psychology Department served as observers. An additional 56 rats, 50–60 days old, that had participated in other experiments served as demonstrators.

Apparatus and diets

We used the same apparatus and diets in experiment 3 that we had used in experiments 1 and 2.

Procedure

Study 1. The procedure we used in study 1 was the same as that used in experiment 2, except that we assigned observers and demonstrators to two conditions that differed in the interval between demonstrations experienced by observers. Observer rats that we assigned to the same-day condition ($N=20$) interacted with two demonstrator rats. Both demonstrators with which any observer interacted had just eaten either diet Cin or diet Coc for 1 h. Observer rats that we assigned to the 24-h condition ($N=22$) also interacted for 30 min with each of two demonstrator rats immediately after each was fed either diet Cin or diet Coc, but each observer assigned to the 24-h condition interacted with its second demonstrator 24 h after it interacted with its first demonstrator.

Study 2. The procedure of study 2 was identical to that of study 1, except that in study 2 (1) observer rats that we assigned to the 7-day condition ($N=26$) interacted for 30 min with a demonstrator rat fed either diet Cin or diet Coc on 2 days separated by a week, (2) observer rats that we assigned to the 24-h condition ($N=30$) interacted for 30 min on 2 successive days with a demonstrator rat fed either diet Cin or diet Coc, (3) we maintained each observer on ad libitum diet Pur between the time of its first and second interaction with its demonstrator, and (4) we offered observers a choice between diets Cin and Coc only after they had interacted with their respective demonstrators for the second time. This last change in procedure was necessary to equate the experience of diets Cin and Coc of observers that we assigned to 24-h and 7-day conditions before we started testing their food preferences.

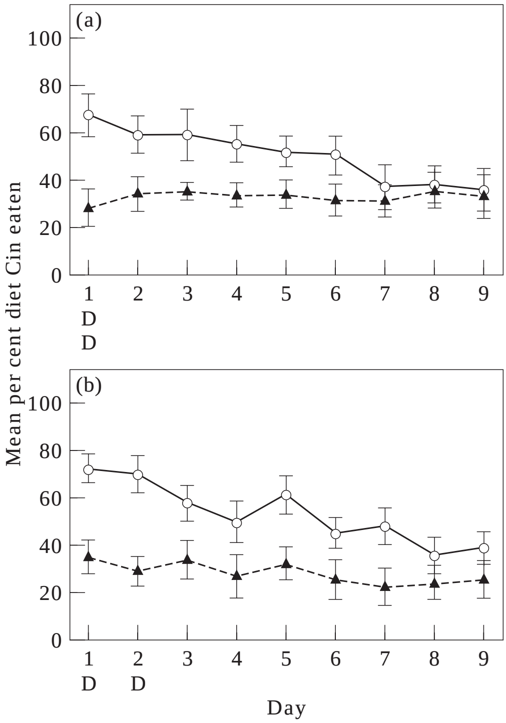

Figure 4. Amount of cinnamon-flavoured diet (diet Cin) eaten, as a percentage of total intake, by observer rats that interacted with (a) on the same day or (b) on 2 successive days with a demonstrator rat fed either diet Cin (○) or diet Coc (▲). D indicates an interaction between an observer rat and its demonstrator.

Data analysis

We analysed the data of experiment 3 as we had done for experiments 1 and 2.

Results and Discussion

The present experiment examined only four of many possible temporal distributions of interactions between demonstrator rats and their observers. Still the outcomes were informative. The results of study 2 (Fig. 3) showed that some temporal distributions of interactions between demonstrator and observer rats were more effective than were others in producing a relatively long-lasting social effect on food choice. Observers that interacted on two occasions separated by 7 days with a demonstrator eating a flavoured diet had less stable preferences for their respective demonstrators' diets than did subjects that interacted twice in 24 h with a demonstrator rat that had eaten the same diets (study 2; $t_{26}=2.15$, $P<0.05$; Fig. 3). On the other hand, we detected no difference in the longevity of the diet preferences induced by two interactions with a single demonstrator on the same or successive days (study 1; $t_{19}=0.60$, NS; Fig. 4).

GENERAL DISCUSSION

The results of these experiments have implications both for future models of social-learning processes and for understanding the origins of stable differences between individuals in patterns of food choice.

Implications for Models

The results of experiments 1, 2 and 3, that both the number of demonstrations an observer receives and the temporal distribution of those demonstrations affect the longevity of socially induced food choices complicates the modelling of social influences on behaviour.

Implications for Traditions of Food Choice

We undertook the present series of studies primarily to examine factors that affect the duration of socially induced preferences for functionally equivalent acts. We found that, under some circumstances, social effects on the food choices of observer rats remained statistically reliable for several days (e.g. Fig. 1c and Fig. 2c, d). Such social effects on food choices are surely sufficiently long-lived to permit propagation of an arbitrary food preference through a population of rats (Galef & Allen 1995). Still, the life span of robust differences between individuals in food preferences resulting from social learning was relatively brief. Consequently, it seems unlikely that the experience of interacting with a demonstrator or series of demonstrators would, of itself, produce a stable pattern of food choice in individual rats.

Although interaction with a demonstrator rat or rats was effective in introducing a bias into the food preferences of observers, the socially induced behaviour appears to have been affected by the relative magnitude of the rewards that resulted from engaging in the socially induced behaviour and its alternative. Individual experience of the roughly equivalent consequences of eating the two foods resulted in extinction of the socially induced preference. Thus, our results are consistent with the hypothesis, that, without environmental support, individuals will express socially learned behaviours for only a relatively short time (Galef 1995, 1996).

Problems with Extrapolation to Free-living Populations

Despite the relatively brief life span of socially induced, arbitrary food preferences shown by Norway rats in the present experiments, it remains possible that social learning could support durable traditions of food preference in populations of free-living animals. Patterns of interaction between the members of a free-living rat colony are surely far more complex than were those between participants in our experiments. In free-living populations, individuals that acquire a food preference as the result of interacting with others might subsequently 're-infect' initiators of the preference that had abandoned it. Thus, at least in principle, a socially induced behaviour could be maintained indefinitely in a population, even if its expression by any single population member is relatively brief. We need to know more, about both patterns of interaction among free-living animals and the probability that individuals are 're-infected' with socially learned behaviours, if we are to extrapolate with confidence from controlled studies of social learning in individuals to social effects on the behaviour of populations of free-living animals.

ACKNOWLEDGMENTS

This research was supported by grants from the Natural Sciences and Engineering Research Council of Canada to B.G.G., Jr. We thank Mertice Clark and Kevin Laland for thoughtful critiques of an early version of the manuscript and an anonymous referee for pointing out problems in extrapolating from our laboratory studies.

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