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SOCIAL INFLUENCES ON THE FOOD PREFERENCES OF HOUSE MICE (*MUS MUSCULUS*)

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ABSTRACT: In a series of studies undertaken to determine the conditions under which naive house mice (observers) develop preferences for foods eaten by recently-fed conspecifics (demonstrators), we found that observer mice exhibited enhanced preference for a food following interaction with either a healthy or an ill recently-fed demonstrator that had eaten that food. We also found that house mice developed an enhanced preference for a food after exposure to an anesthetized conspecific demonstrator powdered with that food, but not after exposure to a cotton-batting, conspecific-sized surrogate powdered with the same food. Results of other studies have indicated that, for both rats and mice, the presence in a food of carbon disulfide (a substance found on the breath of rats) increases preference for a carbon-disulfide-contaminated food. Taken together, the parallels between Norway rats and house mice in social learning processes suggest homologous rather than analogous systems of communication about distant foods in these two murid rodents.

During social contact between a recently-fed Norway rat (a demonstrator) and a naive conspecific (an observer), olfactory cues pass from demonstrator to observer increasing the observer's subsequent preference for the food its demonstrator ate (Galef & Wigmore, 1983; Posadas-Andrews & Roper, 1983). Studies carried out in our laboratory during the past 5 years have provided a detailed picture of both the social interactions and chemical signals responsible for this social influence on diet choice in domesticated rats (For reviews see Galef 1988, 1989a). The experiments described here were undertaken to determine whether the same behavioral processes that support social transmission of information about distant foods in Norway rats (*Rattus norvegicus*) might be found in a second species of myomorph rodent, *Mus musculus*.

House mice, like Norway rats, are members of the subfamily Murinae, the Old World rats and mice. Outside the laboratory, both Norway rats and house mice are social animals, both are dietary generalists, and both are cosmopolitan, human commensals, subjected to human-introduced poisons in many parts of their largely-overlapping species ranges (Nowak & Paradiso, 1983). Most relevant to the present studies, both Norway rats and house mice are social, central-place foragers (Ward & Zahavi, 1973). Members of each species live in fixed home sites from which they emerge to forage and to which they return periodically. Further, because members of both species interact with conspecifics at their respective home sites, they have the opportunity to exploit conspecifics as sources of information about distant foods.

Thus, on both phylogenetic and ecological grounds, one might expect Norway rats and house mice to exhibit similar effects of social influence on their feeding behaviors. In particular, given that rats use conspecifics as sources of information about what foods to eat (Galef, 1989a; Galef & Wigmore, 1983), one might predict that house mice would do so as well. It is not, however, at all clear whether one should expect such phenotypic similarity to extend from overt behavior to underlying process.

If rats and mice share only a tendency to eat what others of their species are eating, then such similarity in behavior might well be a convergent response to similar ecological demands rather than the result of homologous social learning process. On the other hand, if details of the learning processes involved in social transmission of food preferences were identical in rats and mice, it would suggest that social learning about foods was homologous in the two species (Simpson, 1961). The experiments described below were undertaken to determine whether the details of the processes of social influence on food choice of house mice were similar to the processes of social influence on food choice exhibited by Norway rats.

EXPERIMENT 1

In previous experiments concerned with social learning about distant foods by Norway rats (see for example Galef & Wigmore, 1983) food-deprived demonstrator rats were fed either a cocoa- or a cinnamon-flavored diet for 30 min. Each demonstrator was then allowed to interact with an experimentally-naive observer rat for 15 min. Later, when observer rats were offered a choice between cinnamon- and cocoa-flavored diets, they exhibited a robust preference for whichever of the two diets their respective demonstrators had eaten. In the present experiment, we repeated this basic procedure using domesticated house mice rather than domesticated Norway rats as subjects. Our goal was to

determine whether mice, like rats, would use conspecifics as sources of information about which food to eat.

Method

Animals. — Sixteen experimentally-naive, adult female albino mice (*Mus musculus*) of the CD-1 strain (obtained from Charles River Canada, St. Constant, Quebec), weighing 20-25 g, served as observers. Sixteen additional, similar females served as demonstrators.

All animals were housed and tested in temperature- and humidity-controlled animal rooms maintained on a 12-hr light/dark cycle (light onset at 0700 hr). Interactions between demonstrators and observers (see Procedure) were initiated between 1045 and 1100 hr.

Apparatus. — Subjects were housed in demonstrator-observer pairs in 30 x 30 x 15 cm stainless-steel home-cages. Each home-cage was divided into two equal parts by a double-walled, opaque partition. Individual observers were tested for their food preferences in a 32.5 x 37.5 x 16.5 cm plastic, shoebox cage, covered with a 1/4-in. (.62-cm) hardware cloth lid.

To permit precise measurement of food intake, food was presented to both demonstrators and observers in specially-designed feeding devices. Each feeding device was constructed by attaching a 4.5 x 4.5 cm glass jar with a Bakelite lid (in which a 2-cm-diameter hole had been drilled) to the center of a 4 x 8-cm-diameter, Pyrex crystallizing dish (Corning Glass, Corning, NY). The small opening in the food jar reduced spillage of the powdered food each jar contained and any spillage that did occur was almost always trapped in the surrounding Pyrex dish. Data were discarded from two animals that spilled food outside the feeding device.

PROCEDURE

Experiment 1 was conducted in five steps:

Step 1. — Each demonstrator-observer pair was placed together in the same compartment of a home-cage and maintained ad lib on pellets of Purina Laboratory Rodent Chow and water for a 2-day period of familiarization with both partner and apparatus.

Step 2. — To ensure that demonstrators ate when they were given the opportunity to do so, the demonstrator in each pair of subjects was moved in its home-cage to the opposite side of the double partition from its observer and was food deprived for 24 hr.

Step 3. — At the end of this 24-hr period of food deprivation, a weighed feeding device containing either a cocoa-flavored diet (Diet Coc: powdered Purina Laboratory rodent Chow adulterated 2% by weight with sifted Hershey's Pure cocoa) or a cinnamon-flavored diet (Diet Cin: powdered Purina Laboratory Rodent Chow adulterated 1% by weight with McCormick's Fancy Ground Cinnamon) was presented to each demonstrator for 45 min. While demonstrators were eating, the experimenter removed the food from each observer's side of the home-cage. At the end of the 45-min demonstrator feeding period, the experimenter weighed each feeding device on a balance sensitive to 0.1 g.

Step 4. — Each demonstrator was moved back to the side of the home-cage containing its observer pair-mate and demonstrator and observer were allowed to interact freely for 30 min.

Step 5. — Demonstrators were removed from the experiment and observers were placed in the individual, shoe-box, test cages described in *Apparatus*. Each test cage contained two weighed feeding devices, one holding Diet Cin and one holding Diet Coc. Observers were left undisturbed for 24 hr to eat from the two feeding devices.

At the end of this 24-hr test period, the experimenter weighed the feeding devices on a digital balance accurate to 0.1 g and calculated the percentage of each observer's total intake eaten from the feeding device containing Diet Cin.

RESULTS AND DISCUSSION

The results of Experiment 1 are presented in Figure 1, which shows the mean amount of Diet Cin eaten by observers during the 24-hr test period, as a percentage of observers' total intakes during testing. As can be seen in Figure 1, those observers whose demonstrators ate Diet Cin ate considerably more Diet Cin than did those observers whose demonstrators ate Diet Coc (Mann-Whitney U test, $U = 3$, $p < .005$). These results demonstrate that mice, like rats (Galef & Wigmore, 1983), can be influenced in their diet choices by information extracted during a brief period of interaction with recently-fed conspecifics.

An unexpected finding in previous studies of social effects on diet selection by Norway rats is that observer rats developed preferences not only for foods eaten by healthy conspecific demonstrators but also for foods eaten by obviously-ill conspecific demonstrators (Galef, Wigmore & Kennett, 1983). Rats appear to learn from conspecifics what foods to eat, but not what foods to avoid eating. In the present experiment, we determined whether observer mice would prefer or avoid a food eaten by an obviously-ill, conspecific demonstrator with which they interacted.

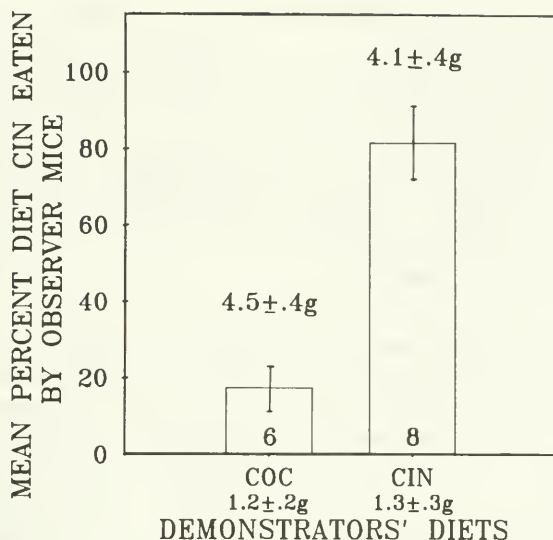


Figure 1

Mean amount of Diet Cin eaten by observers during testing (Step 5), as a percentage of total amount eaten. Bars indicate ± 1 SE; digits in histograms = N/group; numbers above histograms = mean g (± 1 SE) of diet eaten by observers during Step 5 of Procedure. Numbers below abscissa = mean g (± 1 SE) of diet eaten by demonstrators during Step 3.

EXPERIMENT 2

Method

Animals. — Thirty-six experimentally-naive, adult female mice of the CD-1 strain, similar to those used in Experiment 1, served as observers in the present experiment. An additional 36 mice that had served as observers during the previous 2 weeks served as demonstrators.

Apparatus. — The same apparatus was used as in Experiment 1.

PROCEDURE

The procedure was identical to that of Experiment 1 except that immediately following feeding of demonstrators (Step 3 of Procedure), each demonstrator was injected intraperitoneally with either 0.7 cc of .24 M lithium-chloride (LiCl) solution or 0.7 cc of physiological saline. Pilot studies has shown that intraperitoneal injection with such a dose of LiCl produced profound learned aversions in 20-25 g female mice. Adult female CD-1 mice fed Diet Cin and then injected with 0.7 cc of .24 M LiCl solution became lethargic, had severe and conspicuous diarrhea, and

when offered a choice between Diet Cin and Diet Coc 24 hr after injection, ate only Diet Coc.

In the present experiment, half the demonstrators fed Diet Cin and half the demonstrators fed Diet Coc during Step 3 were injected with LiCl solution just before they interacted with their respective observers (Step 4). The other half of each group of demonstrators were injected with saline solution between Steps 3 and 4 of Procedure.

RESULTS AND DISCUSSION

The results of Experiment 2 are presented in Figure 2 which shows the mean percent of Diet Cin eaten during testing by observers that interacted with either saline- or LiCl-injected demonstrators that had eaten either Diet Cin or Diet Coc. As can be seen in Figure 2, during testing, both observers that interacted with LiCl-injected demonstrators and observers that interacted with saline-injected demonstrators showed a marked preference for the diet eaten by their respective demonstrators (Mann-Whitney U tests; see figure 2 for U and p values). As is also evident from inspection of Figure 2, the magnitude of the effects of demonstrators on the food preferences of their respective observers was not affected by the state of health of those demonstrators during the period when demonstrators and observers interacted. Food choices of observer mice, like those of observer rats, were influenced by

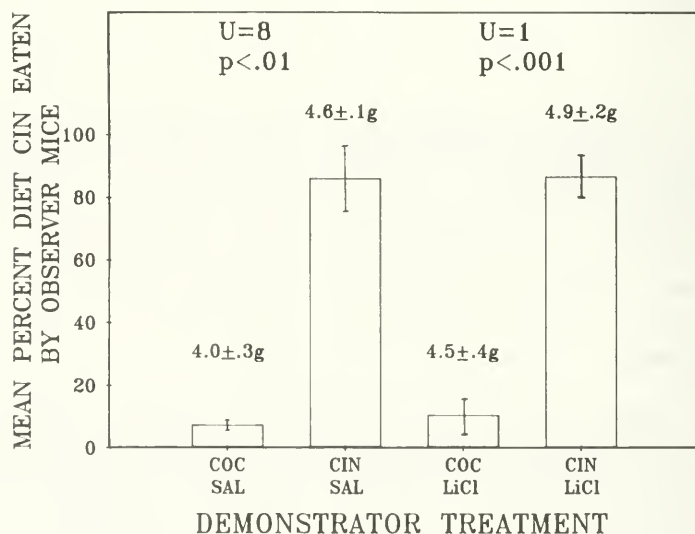


Figure 2

Mean amount of Diet Cin eaten by observers during testing (Step 5) as a percentage of total amount eaten. Bars indicate ± 1 SE; numbers above histograms = mean g (± 1 SE) eaten by observers during testing (Step 5). $N = 9$ observers in each group.

the foods eaten by conspecific demonstrators and not by the health or illness of those demonstrators.

EXPERIMENT 3

The results of previous studies of Norway rats have shown that olfactory signals passing from recently-fed Norway rat demonstrators to their conspecific observers cause the observers to exhibit enhanced preferences for the foods eaten by their respective demonstrators (Galef & Wigmore, 1983). Our data have also indicated that although simple exposure to the taste or smell of a food is often insufficient to enhance the preferences of naive rats for that food, exposure to the same food sprinkled on the face of a demonstrator is sufficient to enhance naive rats' preferences for that food (Galef, 1989b; Galef, Kennett & Stein, 1985; Galef & Stein, 1985).

The present experiment was undertaken to discover whether, for mice as for rats: (a) olfactory cues passing from demonstrator to observer are sufficient to permit demonstrator influence on observer diet preference and (b) the presence of a conspecific demonstrator renders exposure to a food more effective in altering observers' later diet preferences than equivalent exposure to the same food in the absence of a conspecific demonstrator.

Method

Animals. — In the present experiment, 72 experimentally-naive, 20-25 g, female, albino mice of the CD-1 strain served as observers. An additional 52 similar 32-35 g mice, that had been subjects in other experiments, served as demonstrators.

Apparatus. — The apparatus used in the present experiment was the same as that used in Experiments 1 and 2 except during Step 4, the period of interaction of demonstrators and observers. In the present experiment, each demonstrator-observer pair interacted for 30 min in an apparatus constructed from a 2.45 liter (15.2 cm high, 19.0 cm top diam., 14.0 cm bottom diam.) cardboard bucket (Lily-Tulip Inc., Toledo, OH) of the type used by many fast-food franchises. A circular opening (5 cm diam.) was cut in the side of the bucket 12 cm above its floor. Through this opening a cylindrical tube of 1/4-in. (.63-cm) hardware cloth (16 cm long, 5 cm diam.) was inserted for half its length. The end of the cylindrical tube inside the bucket was closed with 1/4-in. (.63 cm) hardware cloth; the end outside the bucket was left open. Cardboard lids prevented observers from leaving their respective buckets (See Figure 4 in Galef, Kennett & Stein, 1985, for an illustration of the apparatus).

PROCEDURE

Steps 1, 2, and 5 in the present experiment were identical to the same steps in Experiments 1 and 2. However in the present experiment, observers interacted with demonstrators during Step 4 in the apparatus described immediately above rather than in their respective home-cages. Further, during Step 3, the demonstrators with which observers interacted during Step 4 were treated in a variety of different ways described below.

Fed-Demonstrator Group (16 observers and 16 demonstrators). — Each demonstrator assigned to the Fed-Demonstrator Group (Fed-Dem Group) was fed either Diet Cin ($n = 8$) or Diet Coc ($n = 8$) for 45 min (Step 3) and was then anesthetized by intraperitoneal injection (60 mg/kg sodium pentobarbital). Each anesthetized demonstrator was placed in a cylindrical, hardware-cloth tube (with its head inside the apparatus) for 30 min to interact with an observer placed in the cardboard bucket.

Powdered-Demonstrator Group (20 observer and 20 demonstrators). — Each demonstrator assigned to the Powdered Demonstrator Group (Powdered-Dem Group) group was not fed during Step 3, but was, instead, anesthetized and had its muzzle powdered with either Diet Cin ($n = 10$) or Diet Coc ($n = 10$). Each demonstrator was then placed in a cylindrical, hardware-cloth tube to interact with an observer placed in the cardboard bucket for 30 min.

Powdered-Demonstrator-on-a-Platform Group (18 observers and 18 demonstrators). — Demonstrators assigned to the Powdered-Demonstrator-on-a Platform-Group (Powdered-Platform Group) were treated identically to those assigned to the Powdered-Dem Group described above except that each demonstrator in the Powdered-Platform Group was fixed with a strip of adhesive tape to a 5 x 16-cm, rectangular piece of plastic that, when placed in the cylindrical, hardware-cloth tube of the apparatus, made impossible direct physical contact between demonstrator and observer during Step 4.

Surrogate-Demonstrator Group (20 observers). — During Step 4, observers assigned to the Surrogate-Demonstrator Group (Surrogate-Dem Group) interacted not with an anesthetized, powdered mouse, but with a mouse-sized, cotton-batting, surrogate mouse one end of which had been powdered with either Diet Cin ($n = 10$) or Diet Coc ($n = 10$). Surrogates were constructed by stuffing an appropriate amount of cotton batting into a length of tubular gauze (Size 12 Tubegauz, School Canada Inc., Toronto, Ont.) and stapling one end of the gauze tube

closed. Surrogate demonstrators were introduced into the cylindrical, hardware-cloth tube with the powdered, closed end inside the bucket and were left there throughout Step 4 of Procedure.

RESULTS AND DISCUSSION

The results of Experiment 3 are presented in Figure 3 which shows the mean percentage of Diet Cin eaten during testing by observers in the various groups.

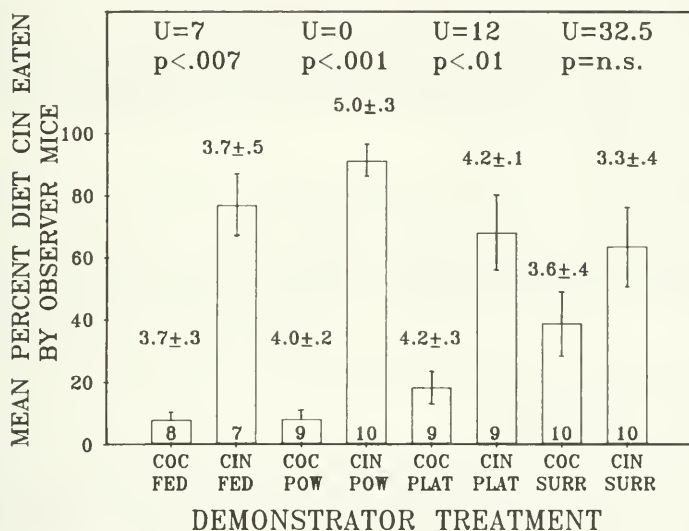


Figure 3

Mean amount of Diet Cin eaten by observers during testing (Step 5) as a percentage of total amount eaten. Bars indicate ± 1 SE; digits in histogram = N/group; numbers above histograms = mean g (± 1 SE) eaten by observers during testing (Step 5).

As can be seen in Figure 3, the diets fed to or powdered on demonstrators in Fed-Dem, Powdered-Dem, and Powdered-Platform Groups had profound effects on the later diet preferences of their respective observers. In each case, those observers interacting with demonstrators fed or powdered with Diet Cin exhibited a greater preference for Diet Cin than did those observers interacting with demonstrators fed or powdered with diet Coc (Mann-Whitney *U* tests, see Figure 3 for *U* and *p* values). As can also be seen in Figure 3, interaction of an observer mouse with a powdered, surrogate demonstrator was less effective in altering observers' diet preferences than was interaction with a powdered, anesthetized demonstrator. The diet powdered onto a surrogate failed to significantly effect observers' subsequent diet preferences.

Several conclusions can be drawn from the results of this experiment. First, the finding that anesthetized demonstrator mice can influence the diet preferences of their respective observers indicates that in mice, as in rats, signals coming from demonstrators that influence an observer's later diet choices are passively emitted by demonstrators rather than elicited by observers.

Second, the observation that demonstrator mice powdered with a diet, rather than fed a diet, affected their observers' later food choices leads to the conclusion that in mice, as in rats, it is not necessary for a demonstrator to eat a food to influence the later food preferences of its observer.

Third, the fact that physical contact between demonstrator and observer was not necessary for induction of changes in the diet preferences of observer mice suggests that in mice, as in rats, olfactory cues emitted by demonstrators suffice to influence the food preferences of their respective observers.

Finally, we found that in mice, as in rats, exposure to a diet powdered on an anesthetized demonstrator, but not to a diet powdered on cotton-battling surrogate, was effective in altering observers' later diet preferences. In both rats and mice the presence of a conspecific appears to be critical in causing exposure to a diet to influence observers' food choices.

GENERAL DISCUSSION

The results of the present series of experiments demonstrate a number of parallels between the processes underlying social influences on diet choice in rats and in mice. Both naive rats and naive mice prefer to eat foods that conspecifics have eaten (Experiment 1); neither avoids foods that ill (Experiment 2) or unconscious (Experiment 3) conspecifics have eaten. Both rats and mice are influenced in their later food choice by the food powdered on a demonstrator, but not by the same food powdered on a cotton surrogate (Experiment 3). Neither rats nor mice require physical contact with a diet-powdered demonstrator to be influenced by it (Experiment 3). Finally, we know from other research that carbon disulfide (a chemical found in rat breath) when added to a food, increased the attractiveness of that food to both rats and mice (Bean, Galef, & Mason, 1988; Galef, Mason, Preti & Bean, 1988; Mason, Bean & Galef, 1989).

Simpson (1961) has proposed that in seeking to identify homologous structures (i.e., those phenotypic characteristics that are similar as the result of descent from a common ancestor) multiplicity of similarities and minuteness of resemblances are important criteria. To date we

have found no differences in the details of either the behavioral processes or chemical signals that support social transmission of diet preference in rats and mice. These findings are consistent with the view that homologous mechanisms operate in social learning about distant foods in two central-place-foraging, generalist, murid rodents, *Rattus norvegicus* and *Mus musculus*.

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