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Social Interaction Modifies Learned Aversions, Sodium Appetite, and Both Palatability and Handling-Time Induced Dietary Preference in Rats (*Rattus norvegicus*)

Bennett G. Galef, Jr.
McMaster University, Hamilton, Ontario, Canada

In a series of four experiments, I examined the extent to which socially transmitted diet preference could counteract the effects of a learned aversion (Experiment 1), a palatability-based diet preference (Experiment 2), a polyethylene glycol 20,000-induced sodium appetite (Experiment 3), and a handling-time induced dietary preference (Experiment 4). I found that (a) rats poisoned after eating a novel diet ate very substantial amounts of the averted diet following interaction with conspecifics that had eaten the averted diet. (b) Following interaction with conspecifics that had eaten an unpalatable diet, rats offered a choice between palatable and unpalatable diets ate more than twice as much unpalatable diet as did controls lacking social experience. (c) Sodium-deficient rats offered a choice between sodium-enriched and sodium-adequate diets ate less than half as much sodium-enriched diet, following interaction with conspecifics that had eaten sodium-adequate diet as did control rats lacking social experience. (d) Rats offered a choice between isocaloric, roughly equipalatable foods with long and short handling times (e.g., sunflower seeds with and without shells) chose the food having the longer handling time after interacting with conspecifics eating that food. These findings suggest that social influence is a major factor in guiding diet selection by rats.

The past two decades have seen publication of a number of studies of social influence on diet selection by Norway rats. Although a variety of ways in which rats can affect the diet choices of conspecifics have been described (for reviews see Galef, 1977, in press), it has been my impression, and I suspect that of others familiar with this work, that social learning is an interesting, but in some sense minor, factor in the development of the feeding repertoires of animals (see, for example, Rozin & Zellner, 1985).

In the experiments reported below, I examined the capacity of one type of social influence on diet preference, the transmission of information about distant diets (Galef & Wigmore, 1983), to modify the effects of other determinants of diet choice: learned taste aversion, palatability-based diet preference, sodium appetite, and handling time.

A naive rat (an observer) that has interacted with a conspecific (a demonstrator) will, when given a choice between two roughly equipalatable, isocaloric diets, exhibit a substantially enhanced preference for whichever of the two diets its demonstrator ate prior to interaction of demonstrator and observer (Galef, 1983; Galef, Kennett, & Wigmore, 1984; Galef & Wigmore, 1983; Posadas-Andrews & Roper, 1983; Strupp & Levitsky, 1984). Olfactory cues passing from demonstrator to observer both identify a demonstrator's diet and provide a social context within which diet-identifying cues experienced by observers are sufficient to enhance observers' subsequent preference for the diet eaten by their respective demonstrators (Galef, Kennett, & Stein, 1985; Galef & Stein, 1985). In this article, I examine the capacity of such socially transmitted information to modify the food choice of observers motivated to eat a diet other than that their demonstrators ate.

In brief, in the experiments described below, I asked four related questions: (a) Will a rat that has learned a toxicosis-induced aversion to a diet eat the averted diet following interaction with conspecifics that have eaten the averted diet? (b) When offered a choice between palatable and unpalatable diets, will a rat choose the unpalatable diet following interaction with conspecifics that have eaten the unpalatable diet? (c) Will a sodium-deficient rat offered a choice between sodium-enriched and sodium-adequate diets eat the sodium-adequate diet after interacting with conspecifics that have eaten the sodium-adequate diet? (d) Will a rat choosing between isocaloric diets having differing handling times (e.g., sunflower seeds with and without shells), choose the diet with the greater handling time after interacting with conspecifics eating that diet? The answers to these questions indicate that social influence is a potent factor in determining diet selection by rats.

Experiment 1

A rat that has ingested a novel diet and then suffered toxicosis exhibits a profound reduction in intake of the

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Correspondence concerning this article should be addressed to Bennett G. Galef, Jr., Department of Psychology, McMaster University, Hamilton, Ontario, L8S 4K1, Canada.

averted diet in subsequent choice situations (Garcia & Hankins, 1977). In the present experiment, rats (observers) were first taught an aversion to a novel, palatable diet and then allowed to interact with conspecifics (demonstrators) that had previously eaten the diet that observers had learned to avoid. Each observer was then offered a choice between the averted diet and a novel food.

Method

Subjects. Seventy-nine 42-day-old female Long-Evans rats acquired from Charles River, Canada (St. Constant, Quebec) served as observers in the present experiment. An additional 54 experimentally naive females, 50–64 days of age, born in the McMaster colony, and descended from Long-Evans stock acquired from Charles River, Canada, served as demonstrators.

Apparatus. Observers were individually housed and tested in 22 × 24 × 27.5 cm wire-mesh hanging cages throughout the 4-day experimental period. Demonstrators were housed individually in plastic shoe-box cages in a room separate from observers.

Procedure. Treatment of observers and demonstrators during the experiment was as follows (see Figure 1):

1. Each observer was placed in a wire-mesh hanging cage and maintained for 24 hr on ad-lib water and Purina Laboratory Rodent Chow pellets.
2. Each observer was then food deprived for 23 hr so that it would eat a novel diet when one was made available.
3. Following food deprivation, each observer was offered, for 1 hr, a weighed sample of a palatable, nutritionally adequate casein and cornstarch based diet, referred to below as Diet NPT (Normal Protein Test Diet; Teklad Test Diets, Madison WI).
4. Immediately following completion of the 1-hr feeding period, each observer was injected ip with 1% body weight of solution: observers in three LiCl groups with 1% w/v LiCl solution, observers in a saline group with isotonic saline solution.
5. One hr following injection, pellets of Purina Laboratory Rodent Chow were returned to each observer's cage, and each was given 23 hr to recover from the effects of injection.
6. Twenty-four hr following injection of observers, each demonstrator (23-hr food deprived and already habituated, for 3 days, to a 23-hr food deprivation schedule) was offered, for 1 hr in its home cage, a weighed sample of Diet NPT.
7. Immediately following feeding of demonstrators, each observer was allowed to interact in its home cage for either $^1/_2$ hr (n = 44) or 1 hr (n = 35) with either (a) a weighed food bowl containing Diet NPT (saline-bowl and LiCl-bowl groups), (b) a single demonstrator that had eaten Diet NPT (LiCl 1-dem groups), or (c) a pair of demonstrators that had eaten Diet NPT (LiCl 2-dem groups). In the last case (c), each of the pair of demonstrators was present in its observer's cage for half of the period of interaction.
8. At the end of the period of interaction, demonstrator or food bowl was removed from the cage of each observer, and each observer was offered a choice, for 22 hr, of weighed samples of Diet NPT and Diet COC (powdered Purina Laboratory Rodent Chow adulterated 2% by weight with Hershey's cocoa).
9. At the end of the 22-hr test, the experimenter weighed both food cups and determined the percentage of Diet NPT eaten by each observer.

Because the experiment required that (a) observers develop an aversion to Diet NPT, (b) demonstrators provide information concerning Diet NPT to observers, and (c) observers choose between diets during testing, 1 discarded data from (a) observers (n = 1) failing to eat 2 g of Diet NPT during Step 3, (b) observers (n = 3) whose demonstrators failed to eat 2 g of Diet NPT during Step 6, and (c) observers (n = 2) failing to eat a total of 5 g of food during testing.

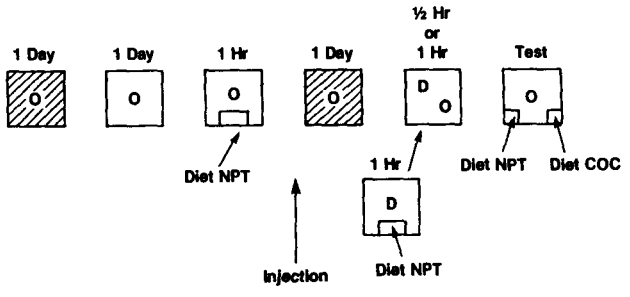

Figure 1. Schematic of the treatment of the LiCl 1-dem group of Experiment 1. (D = demonstrator, O = observer, hatching = ad-lib access to pellets of Purina Laboratory Rodent Chow.)

Results

The main results of Experiment 1 are presented in Figure 2, which shows the amount of Diet NPT, as a percentage of total amount eaten, ingested by observers in the various groups. Comparison of the behavior of subjects in saline-bowl and LiCl-bowl groups indicates that we were successful in inducing an aversion to Diet NPT in both $^1/_2$-hr and 1-hr interaction conditions. In both cases, those observers injected with LiCl solution ate significantly less Diet NPT than did

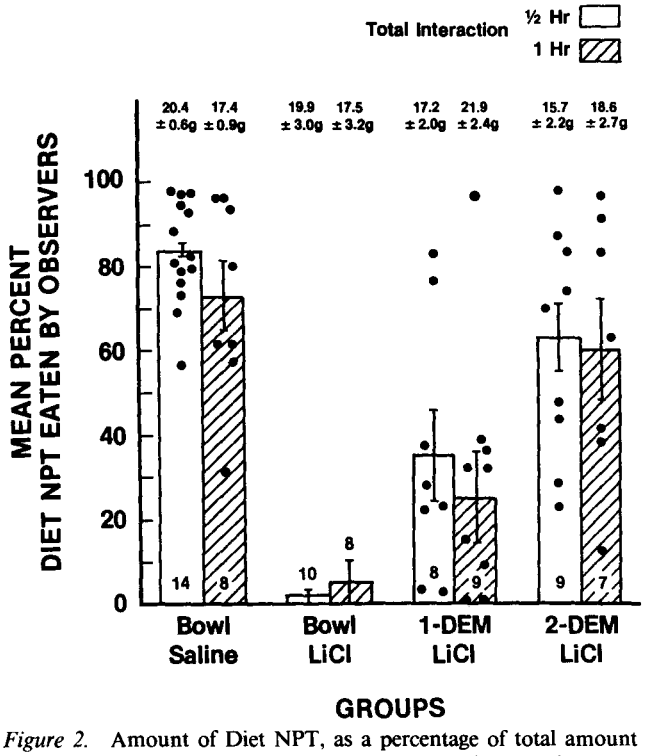

Figure 2. Amount of Diet NPT, as a percentage of total amount eaten, ingested by observers in the eight groups in Experiment 1. (Histograms and flags = $M \pm SE$s. Numbers within histograms = N/Group. Numbers at top of graph = $M \pm SE$s total grams eaten by observers in each group. Open histograms = $^1/_2$ hr interaction during Step 7; stippled histograms = 1 hr interaction during Step 7. For description of treatment of groups see Method of Experiment 1.)

those observers injected with saline solution (Mann-Whitney U tests, both $Us < 2$, both $ps < .001$).

Comparison of the diet selection of subjects in LiCl 2-dem groups with that of subjects in LiCl-bowl groups revealed that interaction for either 1/2 hr or 1 hr with two demonstrators previously fed Diet NPT largely reversed the effects of aversion induction. Observers in both LiCl 2-dem groups ate significantly more Diet NPT than did observers in LiCl-bowl groups (Mann Whitney U tests, both $Us < 3$, both $ps < .001$). Further, comparison of individual data points of observers in LiCl 2-dem groups with those of observers in saline-bowl groups revealed that, for more than half of the observers in each of the LiCl 2-dem groups, the experience of interaction with Diet NPT-fed demonstrators obliterated all trace of aversion to Diet NPT.

Comparison of effects on observer diet choice of interaction with two demonstrators, as compared with one, revealed that interaction with two demonstrators fed Diet NPT was more effective in modifying diet selection than was interaction with a single demonstrator fed that diet (Mann-Whitney U tests, both $Us < 16$, both $ps < .05$).

Examination of diet selection by observers in LiCl-bowl groups indicated that simple exposure to diet-related cues during interaction of demonstrators and observers was not responsible for alterations in observers' diet preferences; observers in both LiCl bowl groups exhibited profound aversions to Diet NPT. Experience of diet-related cues in the presence of demonstrators (LiCl 1-dem and LiCl 2-dem groups) appears necessary for preference alteration in observers (see Galef & Stein, 1985, and Galef, Kennett & Stein, 1985, for further discussion).

Last, duration of interaction (1/2 hr or 1 hr) did not affect the magnitude of demonstrator influence of observers' aversion to Diet NPT. Observers in LiCl 1-dem and LiCl 2-dem groups interacting with demonstrators for 1/2 and 1 hr did not differ in their ingestion of Diet NPT.

Discussion

The results of the present experiment indicate that a rat that has learned an aversion to a palatable diet may abandon that aversion following interaction with demonstrators that previously had eaten the averted diet. Additional studies conducted in our laboratory in which we attempted to increase the proportion of observers exhibiting loss of aversion by (a) increasing the number of demonstrators to three, (b) introducing delays between introduction of successive demonstrators into the cages of observers, and (c) allowing observers to interact simultaneously rather than successively with two or three Diet NPT-fed demonstrators, consistently produced observers 50% of which ingested amounts of Diet NPT comparable with those ingested by saline-injected controls. Effects of demonstrators on observer diet preference were essentially constant in five repetitions. However, in a recent article (Galef, 1985), I reported the results of an experiment similar to the present one, in which effects of demonstrators on their observers' diet preferences following poisoning were smaller than those described here.

I mention this difference in the magnitude of social effects on diet preference in the two series of studies carried out in my laboratory both because it may be of interest to some and because it indicates the difficulties inherent in attempts to assess the relative strength of any two determinants of diet choice. Experimental parameters play an important role in determining which of two influences on diet choice predominate. Hence, the point of the present study is not that social influence is, in some cases, as powerful a factor as taste aversion learning in determining diet choice. Rather, the message to be extracted from these data is that social influence can significantly moderate the effects of toxicosis-induced aversions.

Experiment 2

Diet selection by rats is determined not only by rats' experience of postingestional consequences of ingestion. Diet choice is also strongly influenced by palatability preferences that have been interpreted as reflecting congenital sensory-affective biases of species members developing in normal environments (Cabanac, 1979; Young, 1959, 1968). In the present experiment, I examined the effects of social interaction on such palatability-based diet selection. In brief, observer rats were offered a choice between two novel diets after interacting with demonstrators fed the less palatable of the two. The diets employed in the present study (Diets NPT and COC) have been used extensively in our laboratory for several years, and we have found that female Long-Evans rats eat 3–6 times as much Diet NPT as Diet COC in a choice situation.

Method

Subjects. Fifty-two 42-day-old female Long-Evans rats, acquired from Charles River, Canada (St. Constant, Quebec) served as observers, and an additional 78 experimentally naive 50 to 64-day-old females of the same strain, raised in the McMaster colony, served as demonstrators. (Data from one observer were discarded when one of its demonstrators failed to eat 2 g of diet during Step 2 of the Procedure described below).

Apparatus. The apparatus was the same as that used in Experiment 1.

Procedure. Treatment of observers and demonstrators during the experiment was as follows (see Figure 3):

1. Each observer was placed in a wire-mesh hanging cage and maintained for 48 hr on ad-lib Purina Laboratory Rodent Chow pellets and water.

2. At the end of this 48-hr habituation period, each demonstrator (23-hr food deprived and already habituated for 3 days to a 23-hr food deprivation schedule) was offered a weighed sample of cocoa-flavored diet (Diet COC). While demonstrators were eating, all food was removed from each observer's cage in preparation for interaction of demonstrators and observers.

3. Each observer was allowed to interact for 1 hr with either (a) a bowl of Diet COC (bowl group, $n = 12$), (b) one demonstrator previously fed Diet COC (1-dem group, $n = 12$), (c) two demonstrators previously fed Diet COC and presented in succession to their respective observers for 30 min each (2-dem group, $n = 12$), or (d) three demonstrators previously fed Diet COC and presented in succession to their respective observers for 20 min each (3-dem group, $n = 14$).

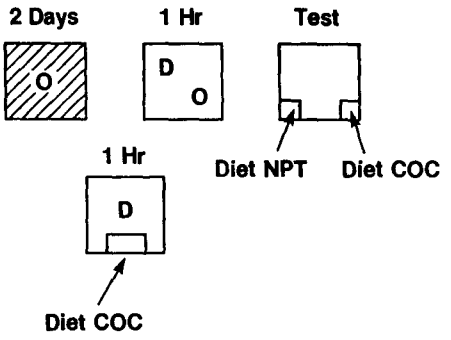

Figure 3. Schematic of treatment of the 1-dem group in Experiment 2. (D = demonstrator; O = observer; hatching indicates ad-lib access to Purina Laboratory Rodent Chow pellets.)

4. At the end of the 1-hr period of interaction, food bowl or demonstrator was removed from each observer's cage, and each observer was offered, for 22 hr, a choice between weighed samples of Diet NPT and Diet COC.

5. At the end of the 22-hr test period the experimenter removed and weighed the food bowls and calculated the percentage of Diet COC eaten by each observer.

Results and Discussion

The main results of Experiment 2 are presented in Figure 4 which shows the mean amount of Diet COC, as a percentage of total amount eaten, ingested by observers in the various groups. As is clear from inspection of Figure 4, observers that had interacted with one, two, or three demonstrators fed Diet COC ate a substantially greater proportion of Diet COC than did observers that had interacted with a food bowl containing Diet COC. Statistical tests revealed that observers in each of the three groups interacting with demonstrators ate significantly more Diet COC than did those observers in the bowl group (Mann-Whitney U tests, all $ps < .01$) but that number of demonstrators did not have a significant effect on the percentage of Diet COC eaten by observers.

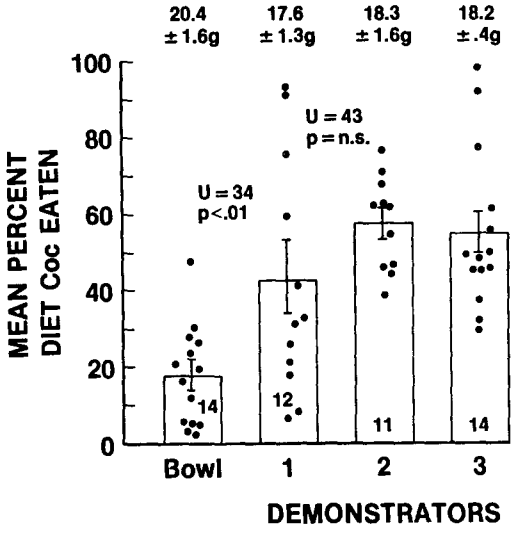

Figure 4. Amount of Diet COC, as a percentage of total amount eaten by observers in Experiment 2. (Histograms and flags = $M \pm SEs$. Numbers within histograms = N/Group. Numbers at top of graph = $M \pm SEs$ of total amount eaten by observers in each group. For description of treatment of groups see Method of Experiment 2.)

The results of the present experiment indicate that social interaction can significantly modify diet selection on the basis of relative palatabilities. Naive rats that have interacted with conspecifics feeding on an unpalatable diet will exhibit an enhanced preference for that diet in a choice situation.

Experiment 3

Rats suffering severe sodium deficiency ingest greater amounts of sodium-enriched diet than of sodium-adequate diet, whereas conspecifics in sodium-balance exhibit the reverse preference (Grimsley, 1973; Richter, 1936).

In the present experiment, I induced a sodium appetite in observer rats by injecting them sc with a hyperoncotic colloidal solution (polyethylene glycol 20,000; Stricker, 1971), let the observers interact with demonstrators eating a flavored, sodium-adequate diet, and then offered the observers a choice between distinctively flavored sodium-adequate and sodium-enriched diets. My goal was to determine whether sodium-deficient rats that had interacted with conspecifics eating flavored, sodium-adequate diet would, in comparison with sodium-deficient control subjects that had not interacted with demonstrators, exhibit reduced intake of flavored, sodium-enriched diet.

Method

Subjects. Forty-eight 42-day-old female Long-Evans rats obtained from Charles River, Canada served as observers, and an additional thirty-two 56–63-day-old females that had served as observers in previous studies served as demonstrators in the present experiment.

Procedure. Treatment of demonstrators and observers in the experimental group (Group PG-2) was as follows (see Figure 5).

1. Each observer was placed in a wire-mesh hanging cage and maintained for 48 hr on ad-lib Purina Laboratory Rodent Chow pellets and water.

2. At the end of this 48-hr habituation period, each observer was anesthetized by ether inhalation and injected sc with 1.6% body weight of either isotonic saline solution or 30% w/v polyethylene glycol 20,000 (BDH Chemicals Ltd., Poole, England) in isotonic saline (Stricker, 1971).

3. Following injection, each observer was returned to its cage and left for 5 hr with ad-lib access to a weighed water bottle, but no food. During the last hour of each observer's 5-hr period of recovery from anesthesia and injection, its demonstrators (already 23-hr food deprived and habituated for 3 days to a 23-hr food deprivation schedule) were fed weighed samples of Diet COC for 1 hr.

4. Immediately following feeding of each demonstrator, it was placed in its observer's cage to interact with its observer for $^1/_2$ hr. Each observer interacted with two demonstrators presented in succession.

5. At the end of the 1-hr period of interaction, each observer was offered, for 17 hr, a choice between weighed samples of Diet COC (powdered Purina Laboratory Rodent Chow adulterated 2% by weight with Hershey's cocoa) and a salt-enriched, cinnamon-flavored diet (Diet CIN + NaCl, powdered Purina Laboratory Rodent Chow

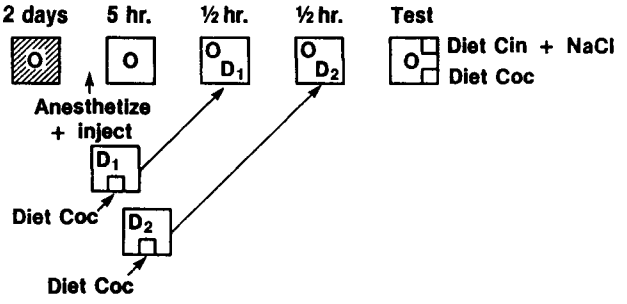

Figure 5. Schematic of treatment of Group PG-2 of Experiment 3. (D = demonstrator; O = observer; hatching indicates ad-lib access to Purina Laboratory Rodent Chow pellets.)

adulterated 1% by weight with McCormick's Pure Ground Cinnamon and 1% by weight with NaCl).

6. At the end of the 17-hr test period, the experimenter weighed each observer's water bottle and food cups and determined both the amount of water drunk by observers during the 22-hr since injection with polyethylene glycol 20,000 and the percentage of salt-enriched diet eaten by each observer during the 17-hr test period. Data from any observer eating less than 5 g during the 17-hr test (n = 3) were discarded.

Subjects in two control groups (Sal-0 and PG-0) were treated identically to those in Group PG-2 with the following exceptions. During Step 2 of the experiment, subjects in Group Sal-0 (n = 16) were injected with 1.6% body weight isotonic saline rather than polyethylene glycol 20,000, and subjects in Group Sal-0 did not interact with demonstrators during Step 4 of the experiment. Data from one subject in Group Sal-0 were discarded because of failure to eat 5 g of diet presented during testing for diet preference (Step 5 of the experiment).

Subjects in Group PG-0 (n = 16) were treated identically to those in Group PG-2, except that subjects in Group PG-0 did not interact with demonstrators during Step 4 of the experiment. Data from 4 subjects in Group PG-0 were discarded because of failure to eat 5 g of diet presented during testing for diet preference.

Results

The main results of Experiment 3 are presented in Figure 6 which shows the mean amount of sodium-enriched diet (Diet CIN + NaCl), as a percentage of total amount ingested, eaten by observers in Groups Sal-0, PG-0, and PG-2 during the 17-hr preference test. The table at the top of Figure 6 shows the mean total amount of food eaten and water drunk by observers in the three groups following injection (Step 2 of the experiment).

Comparison of diet selection by subjects in Groups Sal-0 and PG-0 indicated that we had induced a weak sodium appetite in subjects injected with polyethylene glycol 20,000. Subjects in Group PG-0 ingested significantly greater percentages of sodium-enriched diet (Diet CIN + NaCl) than did subjects in Group Sal-0 (Mann-Whitney U test, U = 49, p = .05).

Comparison of diet selection by subjects in Groups PG-0 and PG-2 indicated that interaction of sodium-deficient observers with demonstrators eating sodium-adequate diet (Diet COC) substantially reduced observer preference for sodium-enriched diet (Diet CIN + NaCl). Taken together, the results of the present experiment indicate that social influence can modify a sodium-deficiency-induced diet preference.

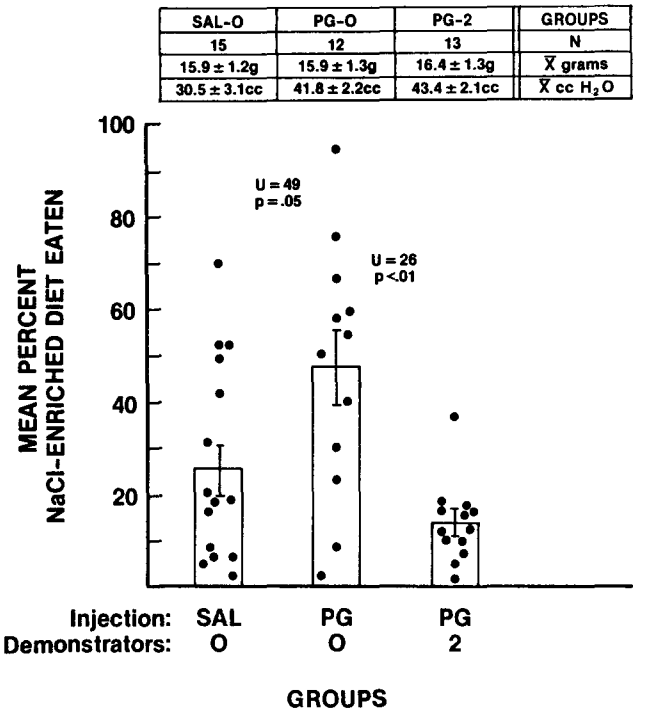

Figure 6. Amount of NaCl-enriched Diet CIN, as a percentage of total amount ingested, eaten by observers in the various groups in Experiment 3.

Discussion

Although results of the present experiment demonstrate a significant reduction in intake of sodium-enriched diet (Diet CIN + NaCl) by sodium-deficient observers following their interaction with demonstrators previously fed sodium-adequate diet (Diet COC), the data are not as convincing as I had hoped. My success in inducing sodium appetite was limited; hence, the present evidence of demonstrator influence on ingestion of sodium-enriched diet by observers is of less interest than it would have been if the sodium-appetite of polyethylene glycol-injected control subjects (Group PG-0) had been greater. The basic problem lay in the fact that rats express salt appetite differently when exposed to salted foods or flavored solutions than when exposed to salted water (Bertino & Beauchamp, 1985).

Almost all published studies of sodium appetite have used as a dependent variable the amounts of saline solutions and water ingested by subjects. I could not use saline solution and water as choice items in the present experiment because, for demonstrators to influence their observers' diet preferences,

the foods fed to demonstrators and offered to observers during testing must differ in odor (Galef & Wigmore, 1983). Further, for purposes of the present experiment, I required diets that, with addition of relatively small amounts of NaCl, both decreased in palatability to sodium-replete rats and increased in palatability to sodium-deficient rats. (If large amounts of sodium were present in the sodium-enriched diet, sodium balance could be restored by sodium deficient rats by ingesting small amounts of sodium-enriched diet.) The present experiment represents my first attempt to identify suitable diets, and I was only partially successful. Evidence of deficiency-induced alterations in diet preference was weak.

Thus, although the data reported here demonstrate that preference for sodium-enriched diets by rats with a weak sodium appetite can be modified by social interaction, generalization of the result to stronger sodium appetites is not appropriate until relevant experiments have been conducted. Students in my laboratory are presently trying to find sodium-enriched diets both more aversive to sodium-replete rats and more preferred by sodium-deficient rats than those diets employed in the present study.

Experiment 4

Optimal foraging theory predicts that animals should select for ingestion those foods that maximize energetic value relative to energetic cost (Emlen, 1966). If faced with a choice between two food items of equal nutritive value that differ only in the time needed to prepare and consume each food item, an animal should preferentially ingest the item with the shorter handling time. For example, rats should, and do, prefer to ingest sunflower seeds without shells rather than those with shells (Kaufman & Collier, 1981).

In the present experiment, rats (observers) were offered a choice between sunflower seeds with and without shells, until they exhibited a stable preference for the latter. They were then allowed to interact with two demonstrators that had eaten either cinnamon-flavored or cocoa-flavored diet. Following interaction with its two demonstrators, each observer was offered a choice between sunflower seeds with shells, flavored as was its demonstrator's diet, and sunflower seeds without shells, flavored with the other flavorant (either cocoa or cinnamon). I determined whether observers that had interacted with demonstrators ate more sunflower seeds with shells than control subjects offered the same food choice as observers, but lacking experience of demonstrators.

The design of the present experiment was constrained by the cost of producing sunflower seeds without shells. Although sunflower seeds with and without shells are readily available commercially, in two pilot experiments, rats offered a choice between sunflower seeds purchased with and without shells clearly preferred those with shells. Apparently, the process used commercially to remove shells from sunflower seeds markedly reduces the palatability of the shell-less sunflower seeds. When I found a third batch of sunflower seeds more acceptable without shells than with them, I could not be certain that this difference in acceptance by rats reflected the presence or absence of shells. The only solution was to remove the shells from a sample of intact sunflower seeds manually to ensure that shelled and unshelled seeds differed only as to the presence of shells. Unfortunately, it takes roughly 54 man-hr/kg to produce sunflower seeds without shells by hand. Various aspects of the procedure reflect the necessity of restricting the use of sunflower seeds without shells to a minimum (approximately 1.4 kg in the present experiment).

Method

Subjects. Thirty-eight 42-day-old female Long-Evans rats served as observers, and an additional 38 females (56–70 days of age) that had served as observers in previous experiments served as demonstrators in the present experiment. Data were discarded from two observers that habitually urinated and defecated on their seeds (preventing accurate determination of intakes) and from three observers that failed to eat 5 g of seeds during testing.

Procedure. Treatment of observers and demonstrators in the experimental group was as follows (see Figure 7):

1. Each observer was placed in a wire-mesh hanging cage and maintained for 24 hr on ad-lib Purina Laboratory Rodent Chow pellets and water.
2. Each observer was then offered for 4 days in succession a choice between weighed samples of sunflower seeds with and without their shells. During this habituation period, and throughout the experiment, pellets of Purina Laboratory Rodent Chow were present in each observer's cage both to provide a nutritionally adequate diet and reduce the number of seeds eaten.
3. Twenty-three-hour-food-deprived demonstrators (already habituated for 3 days to a 23-hr food deprivation schedule) were fed, for 1 hr in a room separate from observers, either Diet CIN (powdered Purina Laboratory Rodent Chow adulterated 1% by weight with McCormick's Pure Ground Cinnamon) or Diet COC (powdered Purina Laboratory Rodent Chow adulterated 2% by weight with Hershey's cocoa).
4. Immediately following feeding of the first of each pair of demonstrators, the sunflower seeds were removed from the cage of its observer, and the first demonstrator was introduced into the observer's cage and left to interact with the observer for $^1/_2$ hr. At the end of the $^1/_2$-hr period, the first demonstrator was removed from and the second demonstrator introduced into each observer's cage for $^1/_2$ hr. Each observer interacted with two demonstrators both of which had eaten the same diet (either Diet CIN or Diet COC) during Step 3 above.
5. Following termination of interaction with its second demonstrator, each observer was offered, for 22 hr, a choice of sunflower seeds with and without shells. Those observers (n = 7) that had

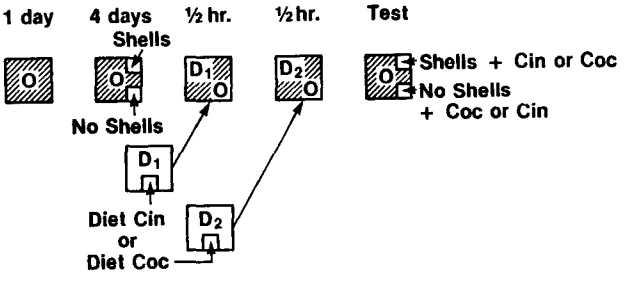

Figure 7. Schematic of treatment of observers in Experiment 4. (D = demonstrator; O = observer; hatching indicates ad-lib access to Purina Laboratory Rodent Chow pellets.)

interacted (Step 4) with demonstrators fed Diet COC were offered sunflower seeds with shells coated with Hershey's cocoa and sunflower seeds without shells coated with McCormick's cinnamon. Those observers that had interacted with demonstrators fed Diet CIN (n = 6) were offered sunflower seeds with shells coated with cinnamon and sunflower seeds without shells coated with cocoa. Coating of sunflower seeds was accomplished by shaking the seeds in a plastic bag with 2% by weight cocoa or 1% by weight cinnamon.

6. At the end of the 22-hr test period, any spillage was returned to the appropriate cups, all husks were removed from the cup containing seeds with shells, and the weight loss of each cup was recorded. The weight loss of the cup containing sunflower seeds with shells was corrected to reflect the edible portion of seeds with shells (0.576), and the proportion of seeds without shells eaten by each observer was then calculated.

Subjects in the control group (0-dem group) were treated identically to observers in the 2-dem group except that no demonstrators were placed in the cages of control subjects during Step 4 of the procedure. During testing, 7 subjects in the 0-dem group were offered sunflower seeds with shells coated with cinnamon and sunflower seeds without shells coated, with cocoa, and 6 subjects in the 0-dem group were offered the opposite combination.

Results and Discussion

The main results of Experiment 4 are presented in Figure 8 which shows the amount of sunflower seeds without shells, as a percentage of total amount of sunflower seeds eaten, ingested by observers with and without exposure to demonstrators. As can be seen in the figure, and as statistical test confirmed (Mann-Whitney U test, $U = 29$, $p < .05$), observers that had interacted with demonstrators ate more sunflower seeds with shells than control subjects lacking such experience. Social influence substantially modified a diet selection on the basis of differences in handling time associated with two roughly isocaloric, equipalatable food items.

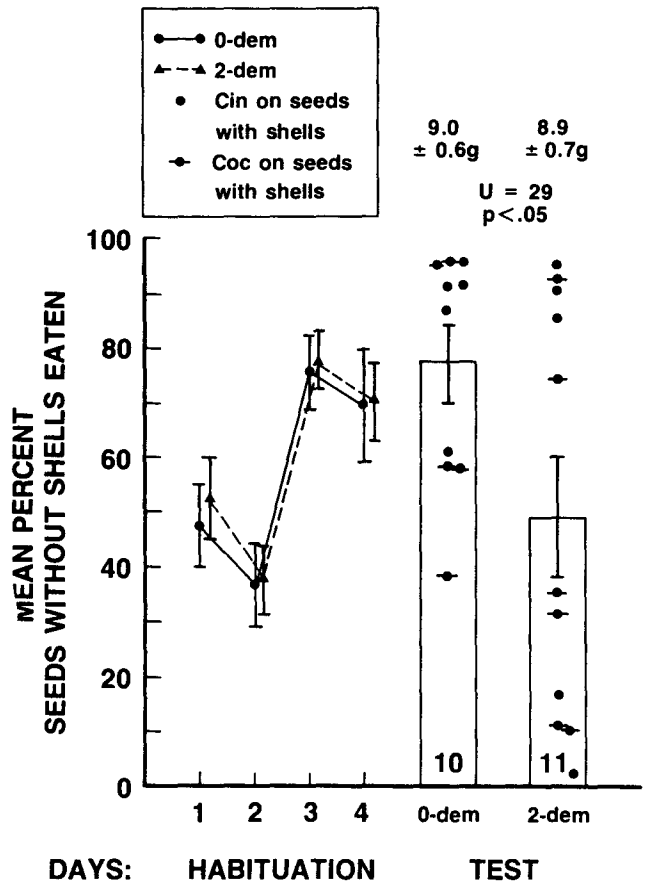

Figure 8. Amount of sunflower seeds without shells eaten, as a percentage of sunflower seeds with and without shells ingested, by subjects in Experiment 4. (Individual data points during testing are identified as to whether subject was offered the choice of cinnamon-coated or cocoa-coated seeds with shells. Numbers at top of graph = $M \pm SE$ of total amount of seeds eaten by observers in each group.)

General Discussion

Taken together, the results of the present series of experiments suggest that social influence plays a more important role in shaping diet selection by rats than has previously been suspected. All major determinants of diet selection examined were significantly modified by social interaction with conspecifics.

Since the 1940s, when systematic study of diet selection in rats was initiated, it has frequently been implicitly assumed that each individual rat has to learn for itself to select those foods needed to sustain growth and life. Individual learning provided the dominant model of development of adaptive patterns of dietary selection in animals.

Rats in natural environments have lived for millenia as members of social groups. The present data indicate that rats have evolved mechanisms, which permit each individual to make use of information concerning the diet selection of its fellow colony members in the development of its own dietary repertoire. It is, thus, no longer necessary to suppose that each new recruit to a rat population must learn for itself the identity of either valuable foods or toxins. Each rat choosing foods for ingestion can make use of information provided by others in its social group already selecting adequate, safe diets. Each rat will abandon, to greater or lesser extent, reliance on information it personally has collected concerning the value of potential ingesta in favor of information acquired from others. In rats, as in humans, social influence is an important determinant of diet selection.

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