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Aversive and Attractive Marking of Toxic and Safe Foods by Norway Rats

BENNETT G. GALEF, JR., AND MATTHEW BECK[1]

Department of Psychology, McMaster University, Hamilton, Ontario, Canada

The present series of studies was undertaken to investigate the hypothesis (von F. Steiniger, 1950, *Zeitschrift für Tierpsychologie*, **7**, 356–379; K. A. Stierhoff, & M. Lavin, 1982, *Behavioral and Neural Biology*, **34**, 180–189) that rats poisoned after eating a novel food will mark that novel food in such a way as to dissuade naive conspecifics from ingesting it. Our results provided no evidence of aversive marking of a novel food by rats poisoned after ingesting it. We did, however, find evidence of attractive marking of feeding sites by rats exploiting those sites. This attractive marking rendered exploited feeding sites more attractive to naive conspecifics than other portions of an enclosure that rats had visited. The present findings are consistent with the results of a number of experiments conducted in our laboratory over the last decade indicating that rats directly communicate learned food preferences, but not learned food aversions. © 1985 Academic Press, Inc.

For more than a decade, our laboratory has been engaged in analyses of social influences on diet selection in Norway rats (*Rattus norvegicus*). In the course of our experiments, we have found four independent ways in which one rat can influence the food preferences of others with which it interacts (Galef & Clark, 1971; Galef & Sherry, 1973; Galef & Heiber, 1976; Galef & Wigmore, 1983). These four behavioral processes, supporting social infuence on diet selection, are similar to one another in that each is sufficient to produce enhanced preference for the diet a conspecific has eaten, while none can directly produce avoidance of a diet that a conspecific has learned to avoid (Galef, in press).

Our laboratory work on social transmission of diet choice in rats was undertaken in response to Steiniger's (1950) field observations indicating that young wild rats will ingest little of a poison bait so long as there

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are present in their colony adults that have learned to reject that bait. Steiniger attributed this avoidance of toxic foods by naive rats to the avoidance-inducing effects of residual chemical cues deposited on poison baits by individuals that had learned to avoid them. Thus, Steiniger hypothesized the existence of a behavioral process resulting in the direct transmission of diet avoidance from one rat to another.

Similarly, Stierhoff and Lavin (1982) have recently suggested that rats made ill by lithium chloride toxicosis may deposit residual avoidance-inducing cues in the vicinity of foods they have learned to avoid. Unfortunately, Stierhoff and Lavin showed only (as have others: Bond, 1982; Coombes, Revusky, & Lett, 1980; Lavin, Freise, & Coombes, 1980), that cues emitted by an ill rat can serve as unconditioned aversive stimuli in a flavor-aversion learning paradigm. They did not demonstrate either that cues produced by an ill rat, adequate to serve as an US in an aversion-learning situation, are differentially deposited in the vicinity of an avoided food or that such deposition would reduce ingestion of the marked food by naive rats. Thus, in spite of suggestions in the literature that rats will mark a toxic food so as to disuade conspecifics from ingesting it, neither evidence for nor direct test of the hypothesis is available in the literature.

The present series of experiments was undertaken to determine whether, as Steiniger (1950) and Stierhoff and Lavin (1982) have proposed, rats that become ill following ingestion of a novel food mark that food or its surround so as to dissuade conspecifics from ingesting the novel food.

EXPERIMENT 1

The first experiment was performed to determine whether rats that eat a novel food at a novel feeding site and then become ill will subsequently mark the novel food with avoidance-inducing residual cues that act to reduce the probability that naive conspecifics will consume the marked food.

Method

Subjects

Twenty experimentally naive 42-day-old Long–Evans rats from the McMaster colony, descendents of breeding stock acquired from Blue Spruce Farms (Altamont, NY) served as naive subjects. An additional 60 similar rats, 90–120 days of age, served as demonstrators.

Apparatus

The present experiment was conducted in 1 × 1 × 0.3-m cages (see Fig. 1A) constructed of angle iron and hardware cloth. Each cage was floored with galvanized sheet metal covered to a depth of 2–3 cm with wood chip bedding and each cage contained a single 30 × 30-cm wooden

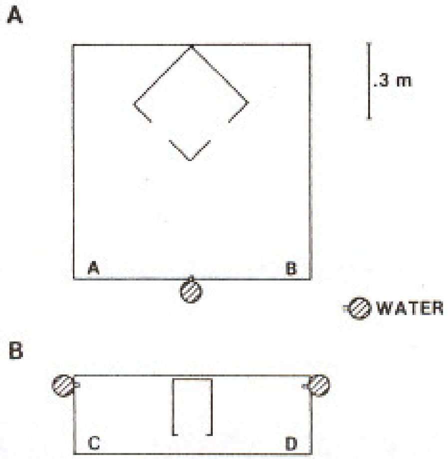


FIG. 1. Overhead schematic of enclosures used in Experiments 1–3 (A) and Experiment 4 (B). The letters A, B, C, and D in the figures represent the location of feeding areas.

nest box with two (5 × 5-cm) entrances, a watering station, and two feeding areas (labeled A and B in Figure 1A).

Procedure

Habituation (Days 1–7). A mixed-sex trio of demonstrator rats was placed in each enclosure and, for 4 days, given ad lib. access to an 11-cm-diam food bowl containing powdered Purina Laboratory Rodent Chow (Diet P) in feeding area A (see Fig. 1A). For the next 3 days, each trio of demonstrators was fed on a 2 h/day feeding schedule, eating Diet P in feeding area A from noon to 2 PM. (To avoid problems of exposition in the description of experiments, we have described procedures as though all rats were habituated to eating Diet P in feeding area A. In reality, the feeding area at which rats were habituated to Diet P and at which other foods were presented was counterbalanced across subjects to control for any positional bias.)

Injection (Day 8). At noon on Day 8 of the experiment, each trio of demonstrators was randomly assigned to Experimental (n = 9 trios) or Control (n = 11 trios) groups. Demonstrator trios in both Experimental and Control groups were given access for 1 h to a weighed food bowl containing a novel diet, Diet NPT (Normal Protein Test Diet: Catalogue No. 170590, Teklad Diets; Madison, WI), placed in a clean food bowl in feeding area B. At the end of this 1-h feeding period, the food bowl was weighed (to ensure that trios of demonstrators had eaten Diet NPT) and returned to its previous position.

Every member of each demonstrator trio was then injected with 1% of body weight of solution: demonstrators assigned to the Control Group with isotonic saline solution and demonstrators assigned to the Experimental group with 2% wt/vol LiCl solution.

Fifteen minutes following injection, the food bowl containing Diet P (from which a demonstrator trio had been eating throughout the habituation phase of the experiment) was returned to feeding area A. Each demonstrator trio was then given $22\frac{3}{4}$ h to feed undisturbed in its enclosure. Control trios were expected to eat both Diet P and the more palatable Diet NPT, Experimental trios to eat Diet P and to avoid (and possibly aversively mark) Diet NPT, ingestion of which had preceded poisoning.

Testing (Days 9 and 10). At noon on Day 9 of the experiment, the food bowl in each enclosure containing Diet NPT was weighed to ensure that members of Control trios had eaten Diet NPT and members of Experimental trios had not. Each trio of demonstrators was then removed from its enclosure and replaced by a single naive rat. At the same time, the food bowl containing Diet P was removed from feeding area A and replaced with a clean food bowl containing a fresh sample of Diet NPT.

Each naive rat was then left to choose between the two food bowls containing Diet NPT: a clean bowl in feeding area A and a bowl in feeding area B that might have been marked by a demonstrator trio during the preceding $22\frac{3}{4}$ h. At the end of the 48-h test period, the amount eaten by each naive rat subject from each of the two bowls containing Diet NPT was determined and the percentage eaten from the bowl in feeding area B was calculated.

Results

During the $22\frac{3}{4}$ h following injection, demonstrators in the Experimental Group ate an average of 0.2 g of Diet NPT, while demonstrators in the Control Group ate an average of 14.8 g of Diet NPT, indicating that the demonstrators in the Experimental Group had, as expected, learned to avoid ingesting Diet NPT, while demonstrators in Control trios had learned to eat that diet.

The main results of Experiment 1 are presented in Fig. 2, which shows the mean amount of Diet NPT eaten from the bowl of diet NPT in feeding area B as a percentage of total amount eaten by naive subjects from both food bowls during their 48 h of testing. As can be seen in Fig. 2: (1) naive subjects in the Experimental Group ate less than half their total intake from feeding area B (Sign test, $x = 1$, $p = .04$), (2) naive subjects in the Control Group ate more than half their intake from feeding area B (Sign test, $x = 1$, $p = .012$), and (3) naive subjects in the Control Group ate a greater percentage of their total intake from feeding area B than did naive subjects in the Experimental Group (Mann–Whitney U test, $U = 8$, $p < .002$).

Discussion

We observed, as Steiniger and Stierhoff and Lavin would have predicted, that naive rats tended to avoid a food bowl containing a novel food that conspecifics had learned to avoid. The findings (1) that naive subjects

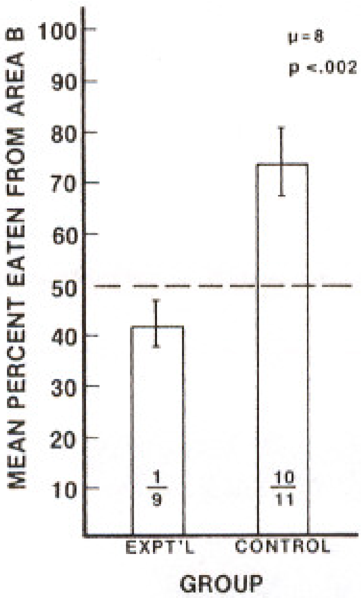
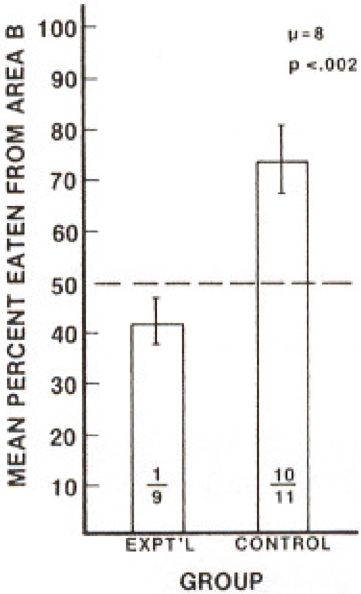


FIG. 2. Mean amount of Diet NPT, as a percentage of total amount eaten, ingested by naive subjects from feeding area B during 48 h of testing. Numbers below the horizontal line within the bars = number of subjects/group. Numbers above the horizontal line = number of subjects eating more than 50% at feeding area B.

in the Experimental Group tended to avoid eating in feeding area B and (2) that naive subjects in the Experimental Group ate a greater proportion of their intake from feeding area B than did naive subjects in the Control Group are consistent with the hypothesis that poisoned demonstrators marked the bowl of Diet NPT in feeding area B so as to induce conspecifics to avoid that bowl. However, the finding that naive subjects in the Control Group exhibited a preference for the food bowl in feeding area B casts some doubt on this interpretation of the behavior of naive subjects in the Experimental Group.

The preference of naive subjects in the Control Group for the food bowl in feeding area B must have been due to attractive residual cues deposited in that bowl or in feeding area B by demonstrator trios in the Control Group during the $22\frac{3}{4}$ h following injection, when they were eating Diet NPT in feeding area B. During the same $22\frac{3}{4}$-h period following injection, demonstrators in the Experimental Group were avoiding the bowl of Diet NPT in feeding area B and were feeding on Diet P in feeding area A, where a clean bowl of Diet NPT was going to be presented to naive subjects. It is thus possible that the apparent avoidance by naive subjects in the Experimental Group of the bowl of Diet NPT in feeding area B was, in fact, the indirect result of attraction to the surround of the clean bowl of Diet NPT in feeding area A. Such attraction would have resulted from the deposition by demonstrators of attractive residual cues in feeding area A during the $22\frac{3}{4}$ h following injection, when they were feeding from the bowl of Diet P located in feeding area A.



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Convincing evidence of the existence of residual cues promoting diet avoidance by naive rats obviously requires controls for the existence of attractive cues, the existence of which is suggested by the behavior of naive subjects in the Control Group of the present experiment.

A further possibility that needs to be considered is that feeding site preference is not the appropriate dependent measure for revealing direct transmission of learned aversions. One might argue that the consequence for a naive rat in the Experimental Group of encountering a food bowl containing Diet NPT and marked by demonstrators with avoidance-inducing cues would be induction of avoidance of Diet NPT in general, rather than induction of avoidance of the particular marked sample of Diet NPT that the naive rat encountered. On this hypothesis, one would predict that naive subjects in the Experimental Group should have eaten less Diet NPT from both feeding sites during the 48-h test period than naive subjects in the Control Group. To the contrary, during 48 h of testing, naive subjects in the Experiment Group ate slightly more Diet NPT ($\bar{X}$ = 26.9 ± 4.8 g) than did naive subjects in the Control Group ($\bar{X}$ = 25.4 ± 3.8 g; Mann–Whitney *U* test, $U = 42$, p = NS).

EXPERIMENT 2

In the present experiment, we again attempted to demonstrate the deposition of avoidance-inducing residual cues in or near a novel food by rats that had learned to avoid that novel food. To remove the ambiguities in interpretation of results present in Experiment 1, we used a procedure similar to that used with the Experimental Group in Experiment 1 while controlling for the presence of residual attractive cues deposited in the vicinity of the clean bowl of Diet NPT in feeding area A prior to introduction of naive subjects into the test enclosure.

Method

Subjects

Thirty three 90- to 120-day-old Long–Evans rats served as demonstrators and 11 additional 42-day-old rats of the same strain served as naive subjects.

Apparatus

The apparatus used was the same as that employed in Experiment 1 except that throughout the 10 days of the experiment each feeding area in the apparatus illustrated in Fig. 1A contained a 30 × 36 × 1.6-cm polypropylene tray covered with wood chip bedding. These trays allowed us to easily manipulate any residual cues deposited in the immediate vicinity of food bowls.

Procedure

Habituation (Days 1–7). During the habituation phase of the present experiment, demonstrator trios were treated in the same manner as were those in Experiment 1. The tray in feeding area A contained a bowl of Diet P and the tray in feeding area B was left empty.

Injection (Day 8). On Day 8 of the present experiment, both the food bowl containing Diet P and the tray beneath it were removed from each enclosure. At the same time, both a clean tray and a clean food bowl containing Diet NPT were placed in feeding area B. One hour later, all demonstrator trios were injected with 1% of body weight, 2% w/v LiCl solution. Fifteen minutes following injection, the tray containing the bowl of Diet P that had been removed prior to the introduction of Diet NPT into each enclosure was returned to its original position (feeding area A) and all trios were then left undisturbed to feed for $22\frac{3}{4}$ h.

Testing (Days 9 and 10). At the end of the $22\frac{3}{4}$-h feeding period, the tray in feeding area A containing Diet P was removed from each enclosure and replaced with a clean tray containing a clean food bowl filled with Diet NPT. In five of the enclosures the two trays and two bowls of Diet NPT were reversed in position; in the other six enclosures the trays and bowls of Diet NPT were left undisturbed.

Demonstrator trios were then removed from each enclosure and replaced by single naive subjects. Naive subjects were left for 48 h to choose between the two feeding areas, one containing a clean tray and a clean bowl of Diet NPT and one containing a tray and a bowl of Diet NPT present in the cage with demonstrators for $22\frac{3}{4}$ h after they were poisoned.

Results and Discussion

If demonstrators had marked the food bowl or tray containing Diet NPT with some avoidance-inducing substance during the $22\frac{3}{4}$ h following poisoning, one would expect naive subjects to exhibit a preference for the clean food bowl on the clean tray during the 48-h testing period. However, as can be seen in Fig. 3, naive subjects exhibited a nonsignificant preference for, rather than an aversion to, the food bowl and tray that had been left with poisoned demonstrators for $22\frac{3}{4}$ h (Sign test, $x = 5$, $p > .05$). As can also be seen in Fig. 3, those naive subjects choosing between trays and food bowls reversed in position prior to testing did not differ in their choice of feeding site from naive subjects choosing between trays and food bowls left in their original positions. One can conclude that food bowl selection by naive subjects was not being affected by residual cues external to the trays themselves. Taken together the results of the present experiment provide no support for the hypothesis that poisoned rats mark a feeding site or food sample that they have learned to avoid with cues that cause conspecifics to avoid that food sample.

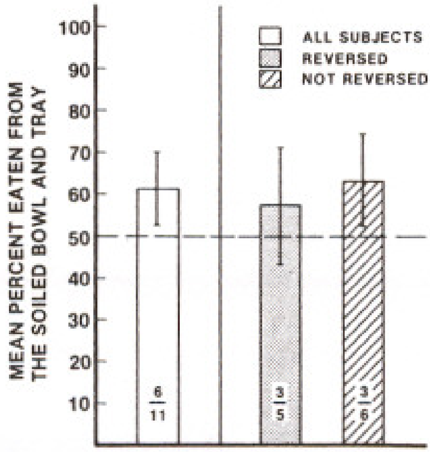

FIG. 3. Mean amount of Diet NPT, as a percentage of total amount ingested, eaten by naive subjects from the soiled bowl and tray during 48 h of testing. See procedure of Experiment 2 for explanation of Groups. Numbers below the horizontal line within bars = number of subjects/group. Numbers above the horizontal line = number of subjects eating more than 50% from the soiled bowl and tray.

EXPERIMENT 3

The behavior of naive subjects in Experiment 2 and in the Control Group of Experiment 1 suggests that both the apparent avoidance of the potentially marked food (in feeding area B) by subjects in the Experimental Group of Experiment 1 and the preference of naive subjects in the Control Group of Experiment 1 for food from the soiled bowl and tray (in feeding area B) were the result of the presence of attractive cues deposited by demonstrators on or near a food they were eating.

The problem with this interpretation is that we have no independent evidence that rats mark feeding sites so as to render them attractive to conspecifics. Galef and Heiber (1976) found that areas in an enclosure that had been explored by adult rats were more attractive to rat pups than clean areas. They were not, however, able to demonstrate that feeding sites were more attractive to rat pups than were other portions of an enclosure that adults had visited. Thus, acceptance of the hypothesis that feeding-site selection by naive rats in Experiment 1 was the result of deposition of attractive cues on or near the sample of Diet NPT eaten by demonstrators requires confirmation.

In the present experiment, we directly tested the hypothesis that rats feeding at some site mark that site so as to make it more attractive to conspecifics than other portions of an enclosure that the rats had visited.

Method

Subjects

Thirty 90- to 120-day-old Long–Evans rats from the McMaster colony served as demonstrators and an additional ten 42-day-old rats of the same strain served as naive subjects.

Apparatus

The apparatus was that of Experiment 2.

Procedure

Habituation (Days 1–7). As in Experiment 2, demonstrator trios were allowed to feed for 7 days on a tray containing a bowl of Diet P placed in feeding area A, while an empty tray was present in feeding area B. At the end of the habituation period the demonstrator trio and food bowl were removed from each enclosure.

A clean food bowl containing Diet NPT was placed in each tray and the trays and food bowls in half the enclosures were reversed in position. A naive subject was then placed in each enclosure and left undisturbed to choose between two clean bowls of Diet NPT, one resting on a tray from which demonstrators had fed and one resting on a tray that demonstrators had visited with some frequency (as evidenced by urine and feces on the tray), but on which they had not fed.

Results and Discussion

Naive subjects ate an average 69.9 ± 9.0% (of their total intake of Diet NPT from feeding area A, where demonstrators had previously eaten, and nine of 10 naive subjects exhibited a preference for feeding from the bowl of Diet NPT on that tray (Sign test, $x = 1$, $p < .01$, two tailed). Clearly, demonstrator trios in the present experiment marked the area around the food bowl from which they were feeding so as to make it more attractive to naive conspecifics than other parts of the enclosure that those demonstrators had explored. One implication of this result is that the finding in Experiment 1 of apparent avoidance by naive subjects of the feeding site avoided by poisoned demonstrator trios could have been the result of an attraction to feeding area A, where poisoned demonstrators fed on Diet P during the $22\frac{3}{4}$ h following injection as well as for the preceding week.

Of course, the existence of attractive cues in one feeding area, sufficient to explain the observed distribution of feeding behavior exhibited by naive subjects in Experiment 1, does not preclude the possibility that poisoned demonstrators in that experiment also deposited avoidance-inducing cues directly in the food that they had learned to avoid. Experiment 4 examines this possibility.

EXPERIMENT 4

In the present experiment, we examined the possibility that demonstrator rats deposit avoidance-inducing residual cues directly on a novel food they have learned to avoid.

Method

Subjects

Thirty three 90- to 120-day-old Long–Evans rats served as demonstrators and an additional 29 similar rats served as naive subjects in the present experiment.

Procedure

A trio of demonstrators was introduced into each of 11 enclosures and habituated (as described in the Method of Experiment 1) to eating Diet P in feeding area A on a 2-h/day schedule.

On the eighth day of the experiment, each demonstrator trio was offered for 1 h a single food bowl containing Diet NPT in feeding area B. At the end of the 1-h feeding period, each member of each demonstrator trio was injected with 1% of body weight 2% (w/v) LiCl solution. Immediately following injection, the food bowl containing Diet NPT was replaced with a clean bowl of Diet NPT (to ensure that any attractive cues deposited in the first bowl of Diet NPT during 1 h of feeding from it prior to injection were removed) and 15 min later a clean bowl of Diet P was placed in feeding area A.

Following placement of the food bowls, each demonstrator trio was left undisturbed to feed and mark as they would for $22\frac{3}{4}$ h.

While demonstrator trios were undergoing the 9 days of procedure described above, 20 naive subjects were habituated to feeding ad lib. on diet P in $1 \times \frac{1}{3}$-m individual enclosures (see Fig. 1B). Twenty-two and three-quarters hours after placement of food bowls in the cages of demonstrator trios, the bowls were removed and the bowl containing Diet NPT was placed in feeding area D of each test cage (see Fig. 1B). At the same time, a clean bowl of Diet NPT was placed in feeding area C of each test cage.

Because pilot studies had revealed a significant preference for feeding at feeding area C by naive rats in these test cages, we also examined the feeding-site preferences of a group of control subjects. These 18 naive rats were simply offered for 48 h a choice between two clean bowls of Diet NPT, one in feeding area C and one in feeding area D.

Results and Discussion

The main results of Experiment 4 are presented in Fig. 4, which shows the mean amount of Diet NPT eaten from feeding area D as a percentage of the total amount ingested by Experimental and Control naive subjects during testing. As can be seen in Fig. 4, Experimental naive subjects ate a slightly greater percentage of their total intake from feeding area D (which contained the food bowl avoided by poisoned demonstrators) than did Control naive subjects. Examination of the food bowls taken

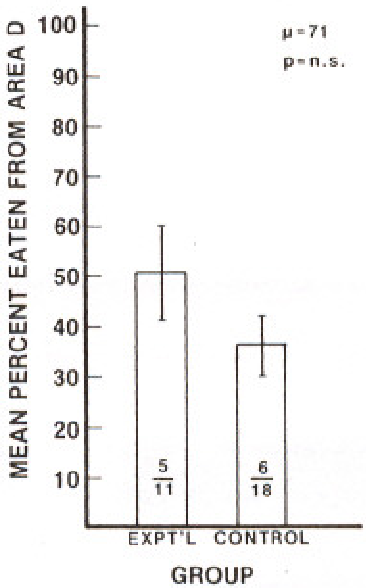

FIG. 4. Mean amount of Diet NPT, as a percentage of total amount ingested, eaten by naive subjects from feeding area D during 48 h of testing. See procedure of Experiment 4 for explanation of groups. Numbers below the horizontal line within bars = number of subjects/group. Numbers above the horizontal line = number of subjects eating more than 50% at feeding area D.

from the cages of poisoned demonstrators and placed in feeding area D revealed that although the demonstrators did not feed from the bowls containing Diet NPT ($\bar{X}$ = 0.1 g) during the 22¾ h following poisoning, they did visit them during the 22¾ h following injection. These visits were indicated by the presence of fecal pellets, hairs, and tracks in the bowls of Diet NPT. Apparently, residual traces of visits to a food cup by poisoned rats tended to make those cups slightly attractive rather than unattractive to naive subjects during their testing.

We were also concerned that the conditions of the present experiment might, for some reason, have been inappropriate to elicit marking behavior by demonstrators. We therefore examined in the apparatus illustrated in Fig. 1B the behavior of two additional groups of naive subjects: a second Control Group (n = 17) choosing between two clean bowls of Diet NPT and an Experimental Group (n = 9) that chose between two bowls of Diet NPT, one in feeding area D that had been eaten from by a trio of demonstrators for 22¾ h and a clean bowl in feeding area C. Naive subjects in the Experimental Condition exhibited a preference for the bowl in feeding area D ($\bar{X}$ = 68.0 ± 6.6%) while those in the Control Group preferred the bowl in feeding area C (61.4 ± 5.9%). Experimental subjects ate a significantly greater proportion of their total intake from the food bowl in feeding area D than did subjects in the Control Group (Mann–Whitney U test, $U = 32, p < .02$). The conditions of the present experiment are clearly adequate to permit marking of a food bowl. Thus, the failure of poisoned demonstrator trios to aversively mark their food cannot be attributed to some general deficiencies in our experimental design.

GENERAL DISCUSSION

The results of the present experiment do not provide any support for the hypothesis that, following the learning of an aversion to a novel food, rats mark that food so as to dissuade naive conspecifics from ingesting it. In two situations in which rats that learned to eat a novel food marked that food or its surround so as to increase the probability that naive conspecifics would feed on it, rats feeding on the same novel food and becoming ill failed to mark that food in such a way as to decrease the probability that naive conspecifics would feed on it.

Although we failed to find evidence of direct transmission of diet aversion, we have uncovered the first evidence of which we know that rats will mark a feeding site or food so as to make them more attractive than other portions of an enclosure in which they are active. This finding, that rats will distinctively mark a feeding site, was unexpected because previous attempts in our laboratory to demonstrate such an effect were unsuccessful (Galef & Heiber, 1976). The reasons for our present success, as contrasted with our past failure, are unknown, but two possibilities suggest themselves. First, the naive subjects used in the Galef and Heiber studies were 16 to 23 days of age, while naive subjects in the present series of studies were 50 days old at testing. The results of several studies (e.g., Leon & Molz, 1972) suggest the existence of age-related changes in the response of rat pups to odors produced by conspecifics. Second, Galef and Heiber (1976) tested their naive subjects in a food-deprived state 1 h/day for 7 consecutive days. In the present experiments we tested replete naive subjects for 48 successive hours. It is possible that food-deprived subjects, exposed to a brief feeding test, are less affected in their choice of feeding site by conspecific odors than are satiated individuals free to spend many hours in choosing a location at which to feed.

The failure of Galef and Heiber (1976) to find evidence of a differential marking of feeding sites and our present success in finding such marking also serves as a potent reminder of the dangers of placing too much emphasis on negative outcomes in work of this type. Some variations in experimental procedure might produce evidence of aversive marking of poisoned foods by knowledgeable rats. However, hypotheses concerning both the existence of behavioral processes (Steiniger, 1950) and functions of demonstrated processes (Stierhoff & Lavin, 1982) should be tested experimentally. In the absence of confirmation, the validity of those hypotheses remains in doubt. The results of the present series of studies fail to provide support for the suggestion that knowledgeable rats mark poison foods so as to dissuade their naive fellows from ingesting them.

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