Demonstration of a socially transmitted taste aversion in the rat

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Observer rats were allowed to interact for 15 min with 2 conspecific demonstrators, 1 that had been fed a cocoa-flavored diet and 1 that had been fed a cinnamon-flavored diet. One of the demonstrators had been made ill immediately following ingestion of its diet. The observer rats were then presented with the cocoa-flavored and cinnamon-flavored diets for 22 h. The observer rats consumed significantly less of the ill demonstrator's diet than of the healthy demonstrator's diet. This finding suggests that, under some conditions, rats can acquire a socially transmitted taste aversion.

There has been considerable interest in the issue of how the behavior of one animal may be affected by its observations of the behavior of a conspecific (e.g., Mineka & Cook, 1993; Pallaud, 1984; Riopelle & Hill, 1973; Robert, 1990; Zentall & Galef, 1988). Investigators have documented both imitative and nonimitative changes in the behavior of an animal following an opportunity to observe the behavior of a conspecific (e.g., Conover, 1987; Curio, 1988; del Russo, 1975; Fiorito & Scotto, 1992; Gaudet & Fenton, 1984; Herman, 1980; John, Chesler, Bartlett, & Victor, 1968; Kawamura, 1963; Mineka, Davidson, Cook, & Keir, 1984; Sherry & Galef, 1984; Veisser & Stefanova, 1993; von Frisch, 1967). One of the most extensively studied cases of nonimitative observational learning involves the transmission of dietary preferences in rats. Following an encounter with a conspecific (demonstrator) that has recently sampled a diet, a rat (observer) will show a preference for the conspecific's diet relative to an unfamiliar diet in a subsequent choice test (Galef, 1983; Galef & Wigmore, 1983; Heyes & Durlach, 1990; Posadas-Andrews & Roper, 1983; Strupp & Levitsky, 1984).

Galef and his colleagues have systematically investigated the conditions under which exposure to a demonstrator conspecific will affect the dietary preferences of an observer rat. A robust preference for the demonstrator's diet has been found across a range of (1) subject variables, such as age, degree of observer-demonstrator familiarity, motivational state, and demonstrator's mode of ingestion of diet, and (2) procedural variables, including duration of observer-demonstrator interaction, dura-

tion and retention of demonstrator-emitted diet-related cues, type of diet, and degree of familiarity with the demonstrator's diet (Galef & Kennett, 1985; Galef, Kennett, & Stein, 1985; Galef, Kennett, & Wigmore, 1984; Galef & Stein, 1985).

Despite the overwhelming evidence for the social transmission of food preferences, it appears that food aversions may not be socially transmitted in rats. An observer rat that has been exposed to a sick demonstrator does not avoid the demonstrator's diet; rather, it shows a significant preference for that diet relative to an unfamiliar one (Galef, McQuoid, & Whiskin, 1990; Galef, Wigmore, & Kennett, 1983). For example, in one experiment reported by Galef et al. (1983), for either 30 min or 2 h, observer rats were allowed to interact with a demonstrator rat that had recently eaten a novel diet (cinnamon- or cocoa-flavored powdered lab chow). Half of the demonstrator rats had received an injection of lithium chloride (LiCl) immediately after eating the novel diet; the others had been given a saline injection. Regardless of whether or not the demonstrator rat was ill during the interaction phase, the observer rats demonstrated a significant preference for the demonstrator's diet relative to an unfamiliar one.

The failure to obtain evidence for the social transmission of a taste aversion may seem surprising for two reasons. First, it has been shown that the diet-related cues emitted by a demonstrator can serve as an effective conditioned stimulus (CS) in a standard taste aversion paradigm (Galef & Kennett, 1985; Galef et al., 1983). Galef et al. (1983) found that an observer rat would subsequently avoid its demonstrator's diet if the observer received an LiCl injection immediately after its exposure to the demonstrator. Second, it has been shown that a rat injected with LiCl can serve as an effective unconditioned stimulus (US) in a standard taste aversion paradigm (Bond, 1982; Coombes, Revusky, & Lett, 1980; Lavin, Freise, & Coombes, 1980; Stierhoff & Lavin, 1982). Lavin et al. (1980) measured saccharin consumption in rats that had previously been given the opportunity to drink a saccharin solution in the presence of either an ill conspecific or a

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healthy conspecific. They found a reduction in saccharin intake in those rats exposed to the ill conspecific.

However, in most studies of the social transmission of a taste aversion, both the CS (diet-related cues) and the US (toxicosis-related cues) emanate from the same animal. As a consequence, the observer's subsequent diet preference will be the product of two antagonistic effects: the social induction of a preference for the demonstrator's diet and the aversion to the demonstrator's diet resulting from exposure to a pairing of the diet-related cues with toxicosis-related cues. Considerable evidence suggests that the former process is particularly powerful. It has, for instance, been shown to undermine existing taste aversions (Galef, 1985, 1986b) and to interfere with the development of new ones (Galef, 1986a, 1987, 1989; Heyes & Durlach, 1990). It is not unreasonable to assume that it may interfere with detection of a socially transmitted taste aversion, particularly when the potential aversion is assessed relative to intake of an unfamiliar diet. One way to address this concern is to modify the testing procedure so that an observer rat is given a choice between two diets, each of which has been eaten by a demonstrator but only one of which has been paired with an ill demonstrator. In this way, intake of both diets will be enhanced by exposure to the demonstrators, but intake of the ill demonstrator's diet should be selectively depressed if an association is formed between that diet and the toxicosis-related cues.

The purpose of the present experiment was to reexamine whether a food aversion might be socially transmitted. Each observer rat interacted with one healthy demonstrator and one ill demonstrator. Immediately prior to this interaction, the demonstrators had been fed one of two diets (a cocoa-flavored diet and a cinnamon-flavored diet). Then, the observer rats were given a choice between the two diets. For each observer, one diet had been eaten by its healthy demonstrator and the other diet by its ill demonstrator. The question of interest is whether observer rats will show a selective aversion to the diet that had been consumed by their ill demonstrators.

METHOD

Subjects

Thirty-two male Holtzman-derived Sprague-Dawley rats (Harlan Co.) served as subjects. They were approximately 190 days old at the start of this experiment and had previously participated in a study of instrumental discrimination learning that used events unrelated to those employed in this study. The subjects were maintained at 80% of their free-feeding weight by limiting their daily access to ProLab Animal Diet pellets. They were housed in individual cages with water always available.

Half of the subjects were randomly assigned to the demonstrator condition and half to the observer condition. Different colored inks were used to mark the tails of the observer rats and the tails of half of the demonstrator rats so that they could be easily identified during the observer-demonstrator interaction phase. Assignment of marked and the trails of unmarked demonstrator rats to specific conditioning treatments was counterbalanced.

Apparatus

Interactions between conspecifics took place in a pen measuring $57 \times 46 \times 19$ cm. The sides of the pen were made of wood, the floor was stainless steel, and the roof was Plexiglas. A layer of cardboard shavings

covered the floor of the pen. These shavings were replaced between each squad of observer and demonstrator rats. All other experimental treatments were conducted in the home cage.

A cocoa-flavored diet was made by combining powdered lab chow with 2% by weight sifted Hershey's cocoa powder. A cinnamon-flavored diet was made by combining powdered lab chow with 1% by weight McCormick ground cinnamon powder. These foods were presented in individual stainless steel cups, measuring $7.5 \times 4 \times 4.5$ cm, that could be hooked to the wire mesh inside the home cage.

Procedure

Half of the subjects were designated as observers, and the other half were designated as demonstrators. The subjects were randomly assigned to one of eight squads, with the restriction that each squad contained 2 observers and 2 demonstrators. Although each squad was run on different days, the procedure for each squad was the same.

Demonstrator treatment. Each demonstrator within a squad was given 20 g of powdered chow on 2 consecutive days. On the 3rd day, each demonstrator was given access to 66 g of either the cocoa-flavored diet or the cinnamon-flavored diet for 1 h in the home cage. To facilitate measurement of any spillage during this exposure period, a clean tray of bedding was placed under the home cages. At the end of the hour, the food dishes were removed from the cages, and 1 of the demonstrator subjects was given an intraperitoneal injection of 5 ml/kg 0.6 M LiCl, a fast-acting toxin. Across the eight squads, half of the injected animals had been fed the cocoa diet and half had received the cinnamon diet.

Interaction phase. Approximately 5 min after the injection, both the injected and noninjected demonstrators were placed for 15 min in the pen with the 2 observer rats assigned to that squad. Each observer was monitored continuously by one of two human observers, who recorded manually the number of contacts that the observer made with each demonstrator. These contacts were classified as "facial" if the observer rat sniffed any part of the head and face of a demonstrator and as "body" if the observer rat sniffed the stomach or anal regions of a demonstrator.

A 15-min interaction period was selected for two reasons. First, a brief interaction period reduced the opportunity for differential exposure to the demonstrators' diets, which has been reported to occur with longer interaction periods (Grover et al., 1988). Second, a brief interaction period ensured exposure of the observer to a pairing of the ill demonstrator's diet with an intense aversive US. Thus, by preventing any recovery of the ill demonstrator in the presence of the observer, the opportunity for any extinction of a learned aversion was limited.

Preference test. At the end of the 15-min interaction phase, all 4 rats were returned to the home cages. For 22 h, each of the observer rats was given access to two food cups, one containing the cocoa diet and one containing the cinnamon diet. These cups were weighed at 30-min intervals during the first 2 h of this test phase and then at the end of the 22-h test.

Following initial training and testing, the entire procedure was repeated with the exception that injections of LiCl were given only to those demonstrators that had not received a previous injection. In this way, each observer rat was exposed twice to the same demonstrator, once when that demonstrator became ill after eating its diet and once when it remained healthy after eating that same diet.

RESULTS

For the purpose of statistical analysis, data were combined across the two cycles of the experiment.

Prefeeding

Every demonstrator rat consumed its daily ration of powdered lab chow. Each demonstrator also sampled a portion of its cocoa-flavored or cinnamon-flavored diet. Moreover, demonstrators' consumption of a diet during the second exposure (17.1 and 16.3 g, injected or not) was not significantly affected by the outcome of the first

Figure 1. Mean consumption (in grams) of the cinnamon-flavored (CIN) and cocoa-flavored (COC) diets as a function of whether the demonstrator rat was healthy (NP) or ill (P).

exposure (18.1 and 14.3 g, injected or not) ($F_s < 1$). Across the two cycles, the mean amounts of cocoa-flavored diet consumed were 17.9 and 17.5 g by demonstrator rats subsequently injected or not; the comparable figures for ingestion of the cinnamon-flavored diet were 17.4 and 13.0 g. A two-way analysis of variance (ANOVA) revealed no significant main effects of either food type (cocoa vs. cinnamon) or conditioning treatment (injected or not); there was no significant interaction ($F_s < 1$).

Interaction Phase

Observer rats explored both facial and body regions of both healthy and ill demonstrator rats. Observer rats made a mean of 4.7 facial contacts and 5.0 body contacts with the healthy demonstrators and a mean of 6.0 facial contacts and 5.8 body contacts with the ill demonstrators. A two-way repeated measures ANOVA revealed no significant main effect of either demonstrator type (healthy vs. ill) or type of contact (facial vs. body) [$F_s(1,15) = 2.88, p_s > .10$]; there was no significant interaction ($F < 1$).

Testing

The results of most interest come from the preference test. The total amounts of cocoa-flavored and cinnamon-flavored diets consumed by the observers are shown in Figure 1. Data are separated as a function of whether the diet had been ingested by the ill or the healthy demonstrator. Although there was an overall preference for the cinnamon-flavored diet relative to the cocoa-flavored diet, it is nevertheless clear that the observer rats consumed substantially less of the diet ingested by the ill demonstrator. A two-way repeated measures ANOVA supports this description. There were significant main

effects of diet type (cocoa vs. cinnamon) [$F(1,15) = 8.67, p < .01$] and demonstrator type (healthy or ill) [$F(1,15) = 7.9, p < .05$]; however, there was no significant interaction [$F(1,15) = 1.95, p > .10$].

A significant effect of demonstrator type was also obtained in an analysis of the amount of cocoa diet consumed expressed as a percentage of the total food eaten in a preference test. The mean percentage of the cocoa-flavored diet eaten by observers following an interaction with an ill cocoa demonstrator and a healthy cinnamon demonstrator was 33.1; the mean percentage of the cocoa-flavored diet eaten by observers following an interaction with a healthy cocoa demonstrator and an ill cinnamon demonstrator was 48.7. A one-way repeated measures ANOVA revealed a significant main effect of demonstrator type (healthy or ill) [$F(1,15) = 6.99, p < .05$].

DISCUSSION

Following a 15-min interaction with 2 demonstrators (1 ill and 1 healthy), observer rats consumed significantly less of the ill demonstrator's diet than of the healthy demonstrator's diet. This aversion to the ill demonstrator's diet suggests that the observer rats associated the diet-related cues with the toxicosis-related cues emitted by the ill demonstrator. To substantiate this interpretation, it would be of considerable interest to examine an observer rat's orofacial responses to its ill demonstrator's diet. Grill and his colleagues (Berridge & Grill, 1983; Pelchat, Grill, Rozin, & Jacobs, 1983; Spector, Breslin, & Grill, 1988) have shown that tastes paired with LiCl toxicosis elicit aversive oromotor and somatic taste reactivity behaviors. Evidence of aversive consummatory responses to the diet paired with the ill demonstrator would help to confirm that a taste aversion may be socially transmitted.

Two aspects of the present design may have been crucial for revealing the social transmission of a taste aversion. First, the observer rats were equally familiar with the two diets in the choice test: Both diets had been presented by conspecifics and, thus, were matched for any social enhancement effect. Moreover, during the interaction period, the observers' exposure to the ill and healthy demonstrators did not differ significantly. If anything, the frequency of facial contacts was higher with the ill demonstrator. Thus, the sensitivity of our testing procedure was optimal for detecting a socially transmitted taste aversion. Second, by restricting interaction with the demonstrators to 15 min, we also ensured a pairing of the ill demonstrator's diet with an intense aversive US. Our brief interaction period, therefore, limited the opportunity for extinction of any learned aversion that might have arisen had the effects of the toxin on the ill demonstrator been allowed to wear off in the presence of the observer. Either or both of these factors may account for why previous efforts to demonstrate a social transmission of a taste aversion in rats have been unsuccessful.

Nevertheless, for several reasons, it seems unlikely that the social transmission of taste aversions would play a significant role in the determination of dietary preferences in the adult rat. In the wild, for example, a rat is unlikely to encounter the ideal conditions needed to support a social transmission of a taste aversion. Moreover, taste aversion learning has been shown to be context specific and to be sensitive to the mode of administration of the toxic diet (e.g., Adams, 1982; Archer, Sjöden, Nilsson, & Carter, 1979, 1980; Sjöden & Archer, 1981). In addition, more difficulty has been reported in conditioning an aversion to an olfactory cue than to a gustatory cue (Hankins, Garcia, & Rusiniak, 1973). Each of these factors might therefore operate to reduce detection or acquisition of a socially transmitted taste aversion in the rat. In summary, although the dietary habits of rats may be influenced occasionally by the malaise experienced by a conspecific, the preponderance of evidence suggests that a rat typically selects the diet eaten by a conspecific with relatively little regard to the postingestional consequences for that conspecific (Galef, 1987; Galef et al., 1990).

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