A Failure to Find Socially Mediated Taste Aversion Learning in Norway Rats (R. norvegicus)

Bennett G. Galef, Jr., Stephen W. Wigmore, and Deborah J. Kennett McMaster University, Hamilton, Ontario, Canada

Observer rats interacted with conspecific demonstrators immediately after demonstrators ate a novel diet and were made ill by LiCl injection. Following their interaction with demonstrators, observers were tested for aversion to their ill demonstrator's diet. Previous research has shown that (a) an observer can extract information from a demonstrator sufficient to permit identification of the demonstrator's diet (Galef & Wigmore, 1983) and (b) a rat ill from LiCl toxicosis is an adequate unconditioned stimulus in a taste aversion learning paradigm (Lavin, Freise, & Coombes, 1980). Further, two of the present experiments demonstrated that cues emitted by a rat, reflecting the particular diet it has eaten, are an adequate conditional stimulus in a toxicosis-induced aversion learning situation. Observer avoidance of a diet previously ingested by an ill demonstrator was, however, not demonstrated. The implications of the failure to find socially mediated aversion learning are discussed.

The results of a number of recent studies demonstrate that signals emitted by rats suffering LiCl toxicosis can serve as unconditioned stimuli in a taste aversion learning paradigm. A rat ingesting some unfamiliar diet prior to exposure to a LiCl-injected conspecific subsequently exhibits reluctance to ingest that diet (Bond, 1982; Coombes, Revusky, & Lett, 1980; Lavin, Freise, & Coombes, 1980; Stierhoff & Lavin, 1982).

Although exposure to an ill conspecific can result in a specific food avoidance in rats in laboratory settings, it is not obvious how such socially mediated taste aversion learning might be used by free-living animals to enhance avoidance of toxic foods. If an unfamiliar food eaten by an individual prior to interaction with an ill conspecific were safe, then subsequent avoidance of that food would be counterproductive. If, to the contrary, an unfamiliar food ingested prior to interaction with an ill conspecific were toxic, then information received from

the ill individual would be redundant. Even in the absence of social learning, a rat ingesting an unfamiliar toxic food would subsequently avoid that food. The functional significance of the potential of ill rats to act as unconditioned aversive stimuli in an avoidance learning situation is not obvious.

Stierhoff and Lavin (1982) suggested that an ill rat may deposit aversion-producing residual odors in the vicinity of a noxious food and that such odors might inhibit ingestion of that food by others of their colony (see also Steiniger, 1950). Unfortunately, Stierhoff and Lavin did not provide evidence either that aversion-producing substances emitted by ill rats directly inhibit ingestion or that rats preferentially deposit such substances in the vicinity of toxic foods.

The results of recent studies both in our laboratory and elsewhere demonstrate that a rat briefly exposed to an unpoisoned conspecific that has eaten some food subsequently exhibits an enhanced preference for that food. One rat can extract information from another concerning the diet the latter individual has recently eaten (Galef & Wigmore, 1983; Posadas-Andrews & Roper, 1983; Strupp & Levitsky, in pressa, in press-b). This finding, taken together with the observation that an ill rat can serve as an unconditioned stimulus for taste aversion learning, suggests that a rat

Requests for reprints should be sent to Bennett G. Galef, Jr., Department of Psychology, McMaster University, Hamilton, Ontario, Canada L8S 4K1.

This research was supported by Natural Sciences and Engineering Research Council of Canada Grant A0307 and McMaster University Research Board grants to B. G. Galef, Jr. We thank Harvey Weingarten and Mertice Clark for their thoughtful commentary on earlier drafts of the manuscript.

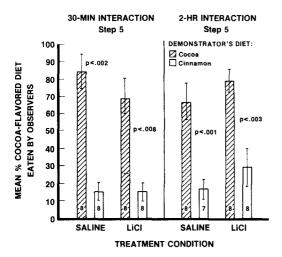


Figure 2. Mean amount of cocoa-flavored diet ingested by observers as a percentage of total amount eaten. (Bars indicate ± 1 SE.)

Results and Discussion

The main results of Experiment 1 are presented in Figure 2, which indicates the mean percentage of cocoa-flavored diet eaten during testing by observers whose demonstrators had eaten either cinnamon-flavored or cocoa-flavored diet. As is evident from inspection of the figure and as statistical tests confirm (Mann-Whitney U tests, see Figure 2 for p values), subjects in both experimental and both control groups exhibited a marked preference for the diet that their respective demonstrators had eaten. Poisoned demonstrators were as effective in promoting intake of the diet they had eaten as were unpoisoned demonstrators.

The failure to find an effect of poisoning demonstrators on their capacity to transfer a preference for the diet they have eaten is open to a variety of intepretations. First, it is possible that although demonstrators emit signals specifying both the food they have eaten and that they have eaten something toxic, observers fail to associate the two messages. Difficulties in forming aversions to demonstrator-produced cues, problems in the temporal patterning of receipt of the two signals, or problems with the relative strength of the preference induced by one signal and the aversion induced by

the other are possible causes of the observed failure of transfer of aversion.

Alternatively, as is the case with all null outcomes, the failure to demonstrate a transfer of aversion from poisoned demonstrators to observers may have been due to our selecting an inappropriate set of experimental conditions. We were, however, careful to select parameters of toxicosis induction in demonstrators and of interaction between demonstrator and observer previously shown to cause observers to learn aversions to unfamiliar foods ingested prior to interaction with a poisoned demonstrator (Bond, 1982; Lavin et al., 1980). Further, the procedures we used were clearly adequate to allow observers to extract information from demonstrators concerning the diets demonstrators had eaten. Conditions were thus appropriate for aversion transfer from observer to demonstrator, yet the anticipated outcome was not observed.

We could continue seeking a set of parameters that would permit socially mediated transfer of aversion, but it is not obvious what conditions to select. We decided instead to ask whether the information extracted by an observer from a demonstrator could serve as the conditional stimulus in a standard aversion learning paradigm. It seemed to us that if an observer could not form an aversion to the food a demonstrator had eaten when that observer was poisoned directly after interacting with a demonstrator fed a novel food, then it was unlikely that under any conditions observers would avoid a food eaten by a demonstrator exhibiting symptoms of toxicosis.

Experiment 2

In this experiment, observers were first allowed to interact with demonstrators fed one of two diets. Each observer was then poisoned by ip injection of LiCl and subsequently offered a choice between the two diets fed to demonstrators.

Method

Subjects. Thirty-two 42-day-old experimentally naive Long-Evans rats from the McMaster colony

made ill following ingestion of a novel food might provide two potentially useful signals to a conspecific: (a) a signal containing information sufficient to permit identification of the food that the signal-emitter has recently eaten and (b) a signal capable of inducing a learned aversion. Exposure to these two signals in temporal contiguity might suffice to produce in their recipient avoidance of the specific diet recently ingested by an ill conspecific.

Experiment 1

Our procedure was designed to mimic a situation in which one rat (a demonstrator) departs from its burrow, ingests a novel toxic food, returns to its burrow, and while suffering toxicosis, interacts with a burrowmate (an observer) which subsequently has the opportunity to ingest the novel food previously eaten by the demonstrator. Our goal was to determine whether such a series of events would result in avoidance by the observer of the food the demonstrator had eaten prior to the onset of toxicosis.

Method

Subjects. Sixty-four experimentally naive Long-Evans rats born in the McMaster colony to breeding stock acquired from Blue Spruce Farms (Altamont, New York) served as observers in the procedure described below. Each observer was 42 days of age at the time of initiation of the experiment. Sixty-four additional 92-day-old Long-Evans rats from the McMaster colony served as demonstrators.

Apparatus. Subjects were housed and tested in same-sex demonstrator-observer pairs in $42.5 \times 24 \times$

27.5 cm wire mesh hanging cages (Wahmann Co., Baltimore, Maryland). Each cage was divided into two equal parts by a 1.25-cm (½-in.) hardware-cloth screen attached to the midpoint of each 42.5-cm side.

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

Step 1: In order to permit familiarization with both apparatus and partner, demonstrator and observer were maintained together with ad lib access to Purina Laboratory Rodent Chow pellets (their normal maintenance diet) and left undisturbed for 2 days.

Step 2: In order to ensure that the demonstrator ate when given the opportunity to do so, each demonstrator was moved to the opposite side of the screen partition from its observer and food deprived for 24 br

Step 3: In preparation for testing of each observer, chow was removed from each observer's side of the apparatus. Each demonstrator was then moved to an individual enclosure in a room separate from that housing the apparatus and allowed to feed for 30 min on either powdered Purina Laboratory Rodent Chow adulterated 2% by weight with sifted Hershey's Pure Cocoa (cocoa-flavored diet) or powdered Purina Laboratory Rodent Chow adulterated 1% by weight with McCormick's Fancy Ground Cinnamon (cinammon-flavored diet).

Step 4: Immediately following termination of Step 3, each demonstrator was randomly assigned to one of two experimental groups or one of two control groups. Demonstrators assigned to experimental groups each received ip injection of 1% of body weight of 2% (w/v) LiCl solution. Members of control groups were injected with an equivalent volume of isotonic saline solution.

Step 5: Immediately following injection, each demonstrator was returned to its respective observer's cage, and demonstrator and observer were allowed to interact for either 30 min or 2 hr, depending on the condition to which a given demonstrator-observer pair had been assigned.

Step 6: Each demonstrator was removed from the experiment, and each observer was offered, for 18 hr, two weighed food cups, one containing cinnamon-flavored diet and one containing cocoa-flavored diet.

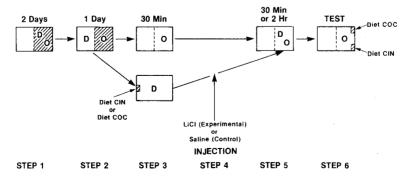


Figure 1. Schematic diagram of the procedure of Experiment 1. (O = observer; D = demonstrator; Diet CIN = cinnamon-flavored diet; Diet COC = cocoa-flavored diet. Hatching indicates pellets of Purina Laboratory Rodent Chow present in cage.)

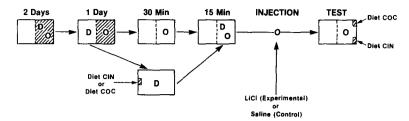


Figure 3. Schematic diagram of the procedure of Experiment 2. (See Figure 1 for abbreviations.)

served as observers, and an additional 32 rats 60-90 days of age served as demonstrators.

Procedure. The procedure (see Figure 3) was similar to that described in Method of Experiment 1 (see Figure 1) except that instead of injecting each demonstrator immediately before it interacted with an observer, we injected each observer immediately after it interacted with a demonstrator. Observers in the experimental group received 1% of body weight of 2% (w/v) LiCl solution; observers in the control group received an equivalent volume of isotonic saline solution. Fifteen minutes following injection, each observer was offered, for 18 hr, a choice between weighed samples of cocoa- and cinnamon-flavored diets.

Results and Discussion

The main results of Experiment 2 are presented in Figure 4 which indicates the percentage of cocoa-flavored diet eaten by observers whose demonstrators had ingested either cinnamon-flavored or cocoa-flavored diet prior to their interaction with observers. During testing, observers in the control group exhibited a preference for the diet their respective demonstrators ate, while those in the experimental group exhibited an aversion to the diet of their respective demonstrators (Mann-Whitney U tests, see Figure 4 for p values).

The results of the present experiment indicate that cues received by observer rats from demonstrators are adequate conditional stimuli for the learning of an aversion. It is, of course, possible that the avoidance of demonstrators' diet exhibited by subjects in the experimental group was not the result of a learned aversion but rather of an unconditioned response to toxicosis. Experiment 3 was undertaken to directly examine the unconditioned effects of toxicosis on observers' preference for demonstrators' diets.

Experiment 3

If the avoidance of demonstrators' diets exhibited by observers were the result of an unconditioned response to toxicosis, one would expect observers poisoned prior to interaction with demonstrators to exhibit an aversion to demonstrators' diets.

Method

Subjects. Twenty-four experimentally naive 42-day-old Long-Evans rats from the McMaster colony served as observers. An additional 24 rats from the same source, 2-3 wk older than observers, served as demonstrators. Half of the observers and half of the demonstrators were assigned to an experimental group; the remainder, to a control group.

Procedure. Treatment of both experimental and control groups is illustrated in Figure 5. In brief, on the third day of the experiment, observers received ip injection of 1% of body weight of a solution. The

OBSERVERS INJECTED

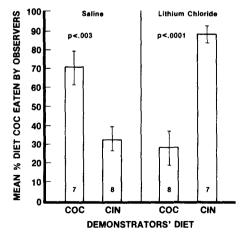


Figure 4. Mean amount of cocoa-flavored (COC) diet ingested by observers as a percentage of total amount eaten. (CIN = cinnamon-flavored diet. Bars indicate $\pm 1 SE$.)

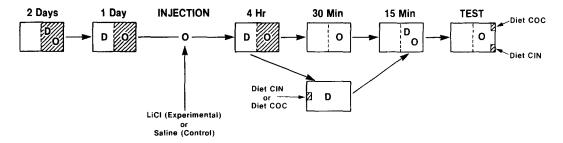


Figure 5. Schematic diagram of the procedure of Experiment 3. (See Figure 1 for abbreviations.)

observers in the control group were injected with isotonic saline, and those in the experimental group with 2% (w/v) LiCl solution. All observers were then left undisturbed for 4 hr while subjects in the experimental group recovered from acute effects of toxicosis induction. Each observer then interacted for 15 min with a demonstrator fed either cinnamon- or cocoaflavored diet, and each observer was subsequently tested for its preference between cinnamon- and cocoa-flavored diets.

Results and Discussion

The main results of Experiment 3 are presented in Figure 6 which indicates the percentage of cocoa-flavored diet eaten by observers whose demonstrators had ingested either cocoa- or cinnamon-flavored diet. During testing, subjects in both control and experimental groups exhibited marked preference for the diet their respective demonstrators had eaten (Mann-Whit-

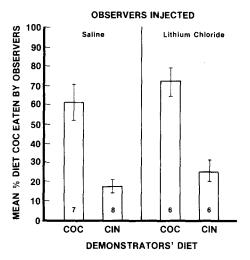


Figure 6. Mean amount of cocoa-flavored (COC) diet ingested by observers as a percentage of total amount eaten. (CIN = cinnamon-flavored diet. Bars indicate \pm 1 SE.)

ney U tests, see Figure 6 for p values). Experience of toxicosis does not in itself result in avoidance by observers of the diet eaten by demonstrators.

General Discussion

The results of the present series of experiments indicate both (a) that cues emitted by one rat, reflecting the identity of the diet that rat has recently eaten, form an adequate conditional stimulus for toxicosis-based aversion learning (Experiments 2 and 3) and (b) that naive rats experiencing the cues emitted by an ill conspecific previously fed a diet do not develop an aversion to that diet (Experiment 1).

Given that the purpose of undertaking this series of studies was to determine whether a rat would avoid ingesting a diet as the result of interacting with an ill conspecific that had ingested that diet, the failure to find such a phenomenon constitutes a null outcome. Like all null outcomes the present finding is difficult to interpret. Taken together, the finding of Lavin et al. (1980), that an ill rat is an adequate unconditioned stimulus for aversion learning, and the finding in Experiment 2 above, that cues emitted by a fed rat are an adequate conditional stimulus for aversion learning, suggest that under the proper set of experimental parameters, one would find socially mediated aversion learning.

Our reason for reporting the present results, rather than searching the relevant parameter space until a situation in which socially mediated aversion learning is obtained, is to make clear that even if the desired result is eventually found, there must be serious question as to its relevance to toxin-avoidance behavior of rats in nat-

ural environments. The more restricted the parameter space in which socially mediated learned aversions occur, the less likely they are to play a role in the diet selection of free-living organisms.

In more than 20 experiments on the socially mediated transfer of diet preference, we have invariably seen preference for demonstrators' diet by observers (Galef, 1983; Galef & Wigmore, 1983). Similarly Strupp (in press-a, in press-b, Note 1) and Posadas-Andrews (1983; Note 2), using quite different experimental paradigms, have repeatedly found social transfer of diet preference. This consistency of outcome across a broad range of conditions suggests that the social transmission of preference for a diet is likely to play a role in natural environments. The difficulty that both our laboratory and that of Posadas-Andrews (Note 2) have experienced in demonstrating socially mediated aversion learning suggests that it is unlikely to be an important aspect of the poison-avoidance behavior of freeliving animals. At the very least, any future demonstration of social transmission by ill rats of an aversion to a specific diet will have to be critically examined to determine whether the parameters allowing such transmission to occur are likely to be found in natural situations.

Reference Notes

 Strupp, B. J. Personal communications, 1982, 1983. Posadas-Andrews, A. Personal communication, 1982

References

Bond, N. W. Transferred odor aversions in adult rats. Behavioral and Neural Biology, 1982, 35, 417-421.

Coombes, S., Revusky, S. H., & Lett, B. T. Long-delay taste-aversion learning in an unpoisoned rat: Exposure to a poisoned rat as the unconditioned stimulus. Learning and Motivation, 1980, 11, 256-266.

Galef, B. G., Jr. Utilization by Norway rats (R. norvegicus) of multiple messages concerning distant foods. Journal of Comparative Psychology, 1983, 97, 364-371.

Galef, B. G., Jr., & Wigmore, S. W. Transfer of information concerning distant foods: A laboratory investigation of the "information-centre" hypothesis. Animal Behaviour, 1983, 31, 748-758.

Lavin, M. J., Freise, B., & Coombes, S. Transferred flavor aversions in adult rats. *Behavioral and Neural Biology*, 1980, 28, 15-33.

Posadas-Andrews, A., & Roper, T. J. Social transmission of food preferences in adult rats. *Animal Behaviour*, 1983, 31, 265-271.

Steiniger, F. von. Beitrage zur Soziologie und sonstigen Biologie der Wanderratte. Zeitschrift für Tierpsychologie, 1950, 7, 356-379.

Stierhoff, K. A., & Lavin, M. The influence of rendering rats anosmic on the poisoned-partner effect. Behavioral and Neural Biology, 1982, 34, 180-189.

Strupp, B. J., & Levitsky, D. A. Early brain insult and cognition: A comparison of malnutrition and hypothyroidism. *Developmental Psychobiology*, in pressa.

Strupp, B. J., & Levitsky, D. A. PKU, learning, and models of mental retardation. *Developmental Psychobiology*, in press-b.

Received April 2, 1983.

Revision received June 16, 1983