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Hungry rats' following of conspecifics to food depends on the diets eaten by potential leaders

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Abstract. Rats *Rattus norvegius*, familiar with maze procedures reliably followed conspecific leaders in a maze. Rats trained to follow in a maze followed leaders that had eaten a food known to the follower to be safe, with higher probability than they followed leaders that had eaten a food known to the follower to be poisonous. Thus, rats have the capacity both to follow conspecifics to feeding sites and to choose conspecifics to follow on the basis of the desirability of the foods those conspecifics have been eating. These findings are consistent with the hypothesis that aggregation sites of rats in natural environments might serve as information centres where unsuccessful foragers could select more successful colony-mates to follow to food.

During a brief period of social interaction, a naive rat (an observer) can acquire sufficient information from a recently fed conspecific (a demonstrator) to permit the observer to identify the diet that its demonstrator ate (Galef & Wigmore 1983; Posadas-Andrews & Roper 1983). Such socially acquired information about diets eaten by demonstrators can be used indirectly by an observer to facilitate its own foraging. An observer that has learned where each of three diets is located, but does not know which diet is available at a given moment, will, after interacting with a demonstrator that has eaten one of the three diets, go to the location where that diet is to be found (Galef & Wigmore 1983; Galef 1984b). Thus, the capacity to identify foods eaten by demonstrators can be used indirectly to orient foraging by an observer that knows the location of a food that a demonstrator has ingested.

The two studies reported below were undertaken to examine the possibility that rats might be able to use information garnered from conspecifics to locate directly those sites where specific foods are available. In experiment 1, we investigated the conditions under which a hungry rat would spontaneously follow a recently fed conspecific to food. In experiment 2, we determined whether hungry rats would follow recently fed rats that had eaten a desirable food more frequently than they would follow recently fed rats that had eaten an undesirable food. Taken together, the results of experiments 1 and 2 indicate that rats have the capacity to

select foraging locations by identifying an individual exploiting a desirable food and then following that individual to that desirable food.

EXPERIMENT 1

A review of the psychological literature indicates that although rats can be trained to follow leaders through a maze by explicitly reinforcing following behaviour, without explicit reinforcement of following, naive rats do not spontaneously follow conspecifics to food (Miller & Dollard 1941; Bayroff & Lard 1951; Solomon & Coles 1954; Church 1957; Stimbert et al. 1966; Stimbert 1969, 1970a, b). There would, obviously, be little point in pursuing the question of whether rats are more likely to follow demonstrators that have eaten a desirable food than to follow demonstrators that have eaten an undesirable food, if rats do not follow one another at all unless taught to do so by an experimenter. Thus, before examining the possible role of diets eaten by potential leaders in eliciting following, it was necessary to determine whether rats would spontaneously follow conspecifics to food.

Informal observations in our laboratory suggested that rats might spontaneously follow one another to food in the absence of formal training to follow. When we tried to conduct studies requiring pairs of rats (one individually trained to go to the left arm and one individually trained to go to the

right arm of a T-maze) to run simultaneously in a maze, both individuals ran to the same arm of the maze on 30% of the trials, even though one or the other lost reinforcement on any trial it entered the same arm of the maze as did its fellow. The failure we experienced during the weeks of training our rats to run reliably to separate arms of the maze suggested both that rats will follow conspecifics in the absence of explicit reinforcement for doing so and that such unreinforced following is difficult to extinguish.

Further, our observations of visits to an artificial feeding site by members of a colony of wild rats, *Rattus norvegicus*, living free in a barn, suggested that the animals were following one another to the feeding site from their burrow system approximately 20 m away. Review of time-lapse videotape recordings of the feeding site revealed that, after many hours had passed without a single rat appearing in the vicinity of the food, as many as six would arrive and begin to eat within a 60-s period. Such simultaneous appearance at a food site could reflect synchronization in feeding rhythms across colony members. However, given the distribution of group appearances at our feeding site this seemed unlikely. Groups frequently appeared in the middle of nocturnal periods of activity, not at sunset, and groups occasionally appeared more than once a night.

Both our difficulties in getting trained rats not to follow one another in a maze and our field observations suggested that rats might follow one another in the absence of training to do so; the psychological literature suggests they do not. In comparing the conditions under which spontaneous following has and has not been observed in laboratory situations, the major difference appeared to us to reside in the familiarity of subjects with the situation in which they were tested for following. Our subjects that refused to go to separate arms of a T-maze and, instead, followed a conspecific had already experienced many trials in the maze during training to go to one arm of the maze.

As mentioned above, other researchers have found that rats reinforced for following conspecifics will do so. During the trials in which rats were being reinforced for following, they were also becoming habituated to maze procedures: handling, the opening and closing of doors, running down alleys, feeding in an unfamiliar location, etc. We, therefore, undertook experiment 1 to deter-

mine whether rats familiar with maze procedures would spontaneously follow conspecifics in a maze in the absence of explicit reinforcement for doing so.

Methods

Subjects

Followers were 10 60-day-old female Long-Evans rats, descended from breeding stock acquired from Canadian Breeding Farms (St. Constant, P.Q.), born and reared in the McMaster colony, and assigned randomly to control ($N = 5$) and experimental ($N = 5$) groups. Four additional females from the same source served as leaders.

Apparatus

All leaders and followers were trained and tested in a four-arm maze designed by Stimbert et al. (1966) and illustrated in Fig. 1 (see Stimbert et al. 1966 for a description). The maze differed from the usual design in having two start-boxes (SB-L and SB-F), one behind the other, and divided goal boxes with separate feeding compartments for leaders (marked L in Fig. 1) and followers (marked F in Fig. 1).

Procedure

Training leaders. Each leader was placed on a 22-h food-deprivation schedule and trained over a
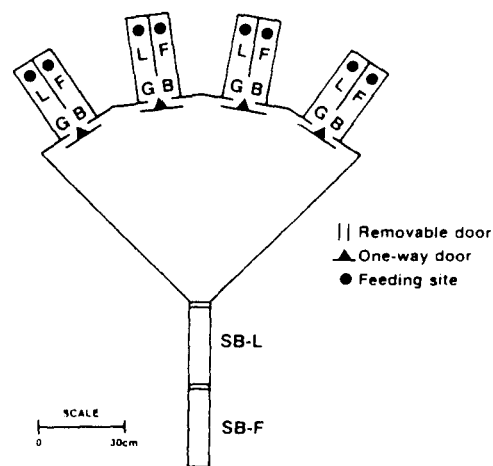
Figure 1. Overhead schematic diagram of the apparatus. SB-L and SB-F = respectively, leaders' and followers' start-boxes, GB-L and GB-F = respectively, leaders' and followers' goal boxes.

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period of 10 days (10 trials/day) to run from SB-L to one of the four goal boxes. For each trial, food (powdered Purina Laboratory Rodent chow) was placed on the L-side of the goal box to which a leader was being trained, the leader was placed in SB-L for 20 s and the guillotine door between SB-L and the body of the maze was opened. If the leader entered the correct goal box, it was allowed to eat for 60 s. If it entered an incorrect goal box, it was left there for 30 s before being returned to SB-L. If a leader failed to enter any goal box within 3 min of the opening of the start-box door, the leader was returned to the start box to initiate the next trial. Each leader was fed powdered Purina Laboratory Rodent Chow in its home cage for 2 h immediately following each day's session in the maze.

Once leaders were running reliably in the maze (nine correct choices out of 10 on 2 consecutive days), each was run for an additional 10 days (10 trials/day) to habituate them to the presence of other rats in the maze. During this phase of leader training, conditions were similar to those prevailing during the first 10 days of leader training, except that, on each trial, a stock rat (an experimentally naive Long-Evans female from the McMaster colony) was placed in SB-F at the start of each trial and both start-box doors were opened to initiate a trial. New stock rats were introduced when their predecessors began to exhibit following.

Training followers. Each of the 10 followers was placed on a 22-h food deprivation schedule for the 16 days it participated in the experiment. On day 8 of deprivation, each follower was habituated to the maze for 1 h with food available in all four goal boxes (in the positions labelled F in Fig. 1) and all doors propped open. On each of days 9 through 16, each follower in the experimental group (*N* = 5), but not the control group (*N* = 5), received eight trials during which it was habituated to maze procedures. On each trial, the follower was placed in SB-F and a diagonally striped 3 × 5 index card was attached to a randomly selected goal-box door. Food was placed only in the F side of the goal box marked with this discriminative stimulus. On each trial, a subject was held in SB-F for 20 s, both start-box doors were opened, and the subject was allowed 3 min to enter a goal box. Choice of the goal box marked by the discriminative stimulus was rewarded with 60-s access to food; entry into any of the other three goal boxes was punished by 30 s of confinement. On the final day of discrimination training, all five subjects in the experimental

group entered a goal box within 15 s of the initiation of each trial, but none showed a significant preference for the stimulus-marked goal box ($\bar{X} = 32.5\%_0 \pm 3.0$ correct responses). Each follower in the experimental group was fed for 2 h in its home cage immediately following its daily sessions in the maze.

Testing followers. On the day following the end of training of followers in the experimental group (day 17 of the experiment), each was run for 12 trials with a leader rat in SB-L. For each trial, one of the four leaders, each trained to go to a different goal box, was placed in SB-L at the same time a follower was placed in SB-F. Reinforcement contingencies were the same as those employed during follower training. A follower was considered to have chosen that goal box into which it first stuck its head even if it pulled back and later entered another goal box. The use of head entry as a criterion of goal box selection by followers prevented followers from scoring well by looking in goal boxes until they found the leader and then entering the goal box occupied by the leader.

Followers in the control group were tested for their tendency to follow leaders in the same fashion as were followers in the experimental group. These control group subjects had been placed on a 22-h food deprivation schedule for 16 days and habituated to the maze for 1 h on the eighth day of the experiment, but had not been subjected to the training in the maze experienced by followers in the experimental group.

Results and Discussion

As can be seen in Fig. 2, followers in the experimental group that had received 56 trials of training prior to testing followed the leaders more frequently than did followers in the control group that lacked training (Mann–Whitney *U*-test; see Fig. 2 for *U*- and *P*-values).

The following that was exhibited by subjects in the experimental group during testing on day 17 cannot be attributed to their generalizing from the discriminative stimulus used during training to the stimuli presented by their leaders during testing. During training, followers had not learned to use the discriminative stimulus to select a goal box to enter.

Our observations of the behaviour of subjects in experimental and control groups during testing for following suggested that experience with maze

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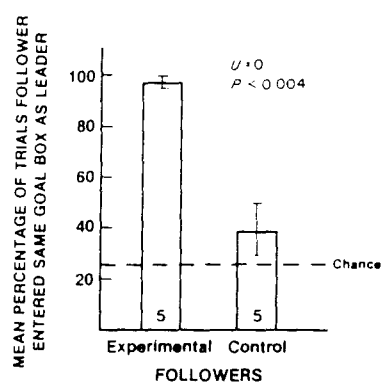
Figure 2. Mean percentage of trials in which followers in experimental and control groups entered the same goal box as their respective leaders during testing. Numbers in histograms = *N* group; flags = ± 1 SEM.

procedures caused experimental subjects to leave the start-box and begin moving towards the goal boxes as soon as the start-box door was opened. Control subjects tended to linger in the start-box before moving into the body of the maze. In consequence, during testing, experimental subjects were moving through the maze at the same time as their respective leaders, while control subjects were not. Thus, each experimental subject was close to its respective leader when the leader entered a goal box. Control subjects did not approach the goal boxes until long after their leaders had disappeared from view into the goal box of their choice.

Regardless of the mechanism proposed to account for the enhancement of following exhibited by followers in the experimental group, it is clear that rats will follow their fellows through a maze in the absence of explicit reinforcement for doing so, if they are familiar with the circumstances in which following is to be tested. This finding suggests that knowledgeable rats might serve their naive fellows as sources of information as to the location at which a desirable food is to be found; the naive rats could simply follow the knowledge-able rats through familiar environments.

EXPERIMENT 2

Efficiency of exploitation of conspecifics as sources of information as to the location of desirable foods would be enhanced if potential followers could select leaders to follow on the basis of the desirabi-

lity of the resource those leaders had been exploit-ing. In experiment 2, we asked whether rats that had learned to follow conspecifics to food would discriminate between potential leaders and select individuals to follow on the basis of the foods potential leaders had eaten.

Methods

Subjects

Four female Long-Evans rats born in the McMaster colony served as leaders and an additio-nal 10 female rats from the same source served as followers.

Procedure

Training leaders. Leaders were trained as de-scribed in the leader training section of experiment 1.

Training followers. Each follower was trained for eight trials/day for 30 days to follow leaders in the maze. Each trial was conducted as described in the leader training section of procedure of experiment 1 except that a follower was placed in SB-F on each trial when a leader was placed in SB-L and food (powdered Purina Laboratory Rodent chow) was available in both sections of the goal box that the leader had been trained to enter on any given trial.

Aversion induction. Immediately following the 26th day of follower training, each follower was given access in its home cage to Diet NPT, a novel, highly palatable, casein and cornstarch based diet (Normal Protein Test Diet, Teklad Test Diets, Madison, Wisconsin, U.S.A.), for 1 h and then poisoned by intraperitoneal injection with 2% of body weight, 2% w v LiCl solution. Poisoning produced a transient disruption of following, so we continued training for an additional 4 days to re-establish high baseline levels of following.

Testing followers. Followers were tested for their ability to select leaders to follow on the basis of the diet that leaders had ingested on the 4 days immediately following the 30th day of follower training. On each test day, each follower was first given four normal training trials (pre-test trials), following one leader to each of the four goal boxes. One leader was then fed in its home-cage on either Diet NPT or powdered Purina Laboratory Rodent chow until it had consumed 2 g. The leader was then placed in SB-L, the follower in SB-F and the opaque guillotine door separating the two start

boxes was replaced with a screen partition. Leader and follower were then left to interact through the partition for 15 min. Following interaction, each follower was run for two trials, using as a leader that individual with which it had interacted during the preceding 15 min. On each trial, the goal box which the leader had been trained to enter contained samples of the diet that the leader had eaten prior to interaction with its follower.

Each follower was tested on 2 days, for a total of four trials, with a leader fed Diet NPT prior to interaction and on 2 additional days, for a total of four trials, with a leader fed Purina Laboratory Rodent chow prior to interaction. Across the 4 days of testing, each follower was tested twice with each of the four leaders. The order of testing with leaders entering each of the four goal boxes and with leaders fed Diet NPT and Purina chow was counterbalanced across followers.

Results and Discussion

As can be seen in Fig. 3, followers were more likely to enter the same goal box as a leader fed Purina Laboratory Rodent chow than a leader fed Diet NPT, the diet followers had learned to avoid. Eight of nine followers were more likely to follow their Purina-chow-fed leaders than their Diet-NPT-fed leaders (sign test, $P < 0.05$). Data from the 10th follower had to be discarded when it failed to
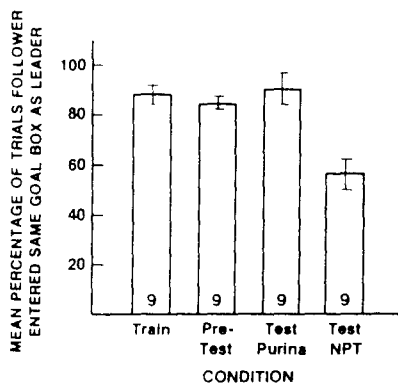
Figure 3. Mean percentage of trials in which followers entered the same goal box as their respective leaders, as a function of leaders' diets during testing: (1) train, the last day of follower training; (2) pre-test, the four pre-test trials run on each day of follower testing; (3) test Purina, the four test trials run following interaction with a leader fed Purina chow; (4) test NPT, the four test trials run following interaction with a leader fed Diet NPT.

exhibit high levels of following towards the end of training, though it too was more likely to follow Purina-chow-fed leaders than Diet-NPT-fed leaders during testing.

Those followers that did follow leaders into goal boxes containing Diet NPT invariably refused to eat Diet NPT during the 60 s they were left in the goal box. Further, 24-h choice tests between Diet NPT and Purina Laboratory Rodent chow, carried out on all followers after the completion of the experiment revealed that all had a preference for Purina chow ($\bar{X} = 71.3\% \pm 6.3$ SE). Ten naive rats offered a 24-h choice between Purina chow and Diet NPT exhibited strong preferences for Diet NPT ($\bar{X} = 81.6\% \pm 3.4$ SE). Thus, our aversion-induction procedure was successful.

GENERAL DISCUSSION

The results of experiment 1 indicate that hungry rats will follow other rats on foraging trips through a maze when familiar with maze procedures, but not when unfamiliar with those procedures. The results of experiment 2 indicate that rats trained to follow leaders are more likely to follow those leaders that had recently eaten a desirable food than to follow those leaders that had recently eaten an undesirable food. Taken together, these data indicate that naive rats have the capacity to use their more-knowledgeable fellows as sources of information as to the locations at which desirable foods are to be found; naive rats will follow conspecifics en route to food and can choose conspecifics to follow on the basis of the desirability of the food those conspecifics have recently eaten.

Of course, the finding that rats in a laboratory situation demonstrate capacities that would enable them to use information acquired from conspecifics to locate desirable foods in natural environments does not mean that rats actually employ those capacities in complex situations outside the laboratory. In spite of our best efforts over two summers, we have not been able to implement studies in a natural setting that might provide evidence that rats discovering a novel feeding site containing a highly palatable diet will recruit colony-mates to that feeding site. Difficulties in capturing, permanently marking and observing animals as neophobic, cautious and wary as wild-living Norway rats presented practical problems

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that we could not overcome with the resources available to us. Testing the hypothesis that free-living wild rats follow conspecifics to food, employing the capacities we have demonstrated in the laboratory, while simple in principle, has proven difficult in practice.

The demonstration that rats have behavioural capacities permitting exploitation of conspecifics as sources of information concerning the location of desirable foods is consistent with the hypothesis that rat colonies serve as information centres (Ward & Zahavi 1973) where relatively unsuccessful foragers could acquire information from their more successful colony-mates as to the location of desirable foods. Of course, extrapolation from a demonstrated capacity in the laboratory to the use of that capacity in the field must be made with caution (Galef 1984a). Our results suggest, but do not show, that free-living rats can exploit their fellows as sources of information as to the location in which desirable foods are to be found.

ACKNOWLEDGMENTS

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