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Use of foraging trails by Norway rats

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Abstract. Six experiments were undertaken to explore the effects of residual trails deposited by one Norway rat, *Rattus norvegicus*, on subsequent choice of path by conspecifics. A rat moving away from (but not towards) a feeding site deposited a trail that biased path choice by its fellows. The relative attractiveness of a trail was affected by the number of times it had been traversed by a rat on its way to and from food, but not by the amount of food a rat ate before depositing a trail. There was no evidence that trails contained information that would allow a rat to move directly towards food rather than directly away from it. Possible sources of the trails deposited by Norway rats as they leave feeding sites are discussed.

Norway rats, *Rattus norvegicus*, can use information acquired from conspecifics to locate feeding sites and to guide response to potential foods (reviewed in Galef 1986; Galef & Beck 1990). Experimental evidence indicates that such social effects on feeding can proceed via five independent routes. (1) While still in utero fetal rats can detect and become familiar with the flavours of at least some of the foods that their dam is eating (Hepper 1988). (2) Flavours of foods ingested by a mother rat are conveyed to her young in her milk, and, at weaning, rat pups prefer foods with flavours that they experienced while nursing (Galef & Henderson 1972; Galef & Sherry 1973; Bronstein 1975; Martin & Alberts 1979). (3) When seeking their first meals of solid food, weaning rats are attracted by the sight of adult conspecifics, approach adults of their species and eat solid food for the first time while in their immediate vicinity (Galef 1971; Galef & Clark 1971a, b). (4) While eating, rats deposit residual olfactory cues both in and around foods, and rats seeking food prefer scent-marked foods and scent-marked feeding sites to unmarked ones (Galef & Heiber 1976; Galef & Beck 1985; Laland & Plotkin 1991, 1993). (5) Finally, by smelling the breath of conspecifics, rats can determine what foods their fellows have been eating and, after detecting a food on the breath of a conspecific, show increased preference for that food (Galef & Wigmore 1983; Galef & Stein 1985; Heyes & Durlach 1990).

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Observations of the behaviour of free-living, wild Norway rats as they move about their home ranges indicate that, outside the laboratory, rats may use a sixth source of social information to increase their foraging efficiency. When moving between foraging and harborage sites, Norway rats tend to follow trails made by others of their colony (Calhoun 1962; Telle 1966). Here, we describe the results of laboratory studies of the effects of trails deposited by Norway rats as they move to and from a feeding site on subsequent path choices by their fellows.

EXPERIMENT 1: DO RATS FOLLOW WELL-ESTABLISHED TRAILS?

Experiment 1 was undertaken to determine whether, in the laboratory, naive rats would tend to follow a well-established trail laid down by conspecifics on their way to and from a feeding site.

Methods

Subjects

Two female Long-Evans rats, 50 days of age at the start of the experiment, served as leaders. We maintained these leader rats on a 23-h per day schedule of food deprivation and fed them powdered Purina rodent laboratory chow daily for

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1 h immediately following their participation in the experiment. An additional 35 42–48-day-old, experimentally naive, virgin female Long-Evans rats served as followers. To reduce variability in behaviour, we used rats of only one sex as followers and rats of the same sex as leaders and followers. The choice of females as subjects was arbitrary.

All 37 subjects were born and reared in the vivarium of the McMaster University Psychology Department (Hamilton, Ontario), and all were descendants of breeding stock acquired from Charles River Canada (St Constant, Quebec).

From weaning until the start of the experiment, we reared all subjects in same-sex groups of three or four siblings and maintained them on ad libitum Purina rodent laboratory chow and water in a temperature- and humidity-controlled colony room.

Apparatus

We conducted experiments in a T-maze constructed of transparent Perspex. The start box of the maze, measuring 15 × 14 × 30 cm, opened via a guillotine door onto a 79-cm-long alley that led to two 61-cm-long arms. A food cup was located on the wall at the end of each arm of the maze, and a guillotine door at the entrance to each arm allowed us to control subject access to that arm.

The maze had two unusual features: (1) it contained a food cup mounted on the wall of the start box opposite the start-box door, and (2) the floor of the maze was made of five pieces of Perspex that could be removed for cleaning.

Procedures

Training leaders. Using ordinary shaping procedures, we trained one leader rat to leave the start box of the maze as soon as the guillotine door was opened, to run to the left arm of the maze and then, after eating from the food cup located there, to run back to the start box and eat from the food cup located there. Using similar methods, we trained the other leader rat to run from the start box to the right arm of the maze, to eat in the right arm of the maze and then to run back to the start box and eat. We ran leader rats for many tens of trials in the maze before starting experiments.

Deposition of trails by leaders. To begin the experiment, we cleaned the maze very thoroughly, first with tap water then with a solution of 50% alcohol and tap water. We then closed off the left arm of the maze, placed the leader rat trained to go to the right arm of the maze in the start box, opened the start-box door and allowed her to make 10 trips to the food cup in the right arm of the maze and back, rewarding her with four, 45-mg food pellets (A/1 rodent pellets, P. J. Noyes, Lancaster, New Hampshire) each time that she encountered a food cup that was on her assigned route. We removed the leader from the apparatus as soon as she had completed her tenth trip back to the start box.

Testing followers. Immediately after we had removed the leader rat from the maze, we introduced a naive follower rat into the start box, opened the start-box door and left the room containing the maze. We then watched on closed circuit television for 5 min to see which arm of the maze the follower rat entered. A follower rat was considered to have entered an arm of the maze when both of its forefeet crossed a line that we had drawn at right angles to the major axis of, and 15 cm inside, each arm of the maze. We eliminated any subject that failed to enter an arm of the maze before the end of a 5-min trial because such subjects did not show a choice and, therefore, did not allow us to score their behaviour with respect to our dependent variable.

As soon as a follower rat entered an arm of the maze (or 5 min had passed), we removed her from the maze and placed another follower rat in the start box. We tested five followers in succession, then removed the floor of the apparatus and washed it, first with a solution of 50% alcohol and tap water, then with tap water.

The next day, we repeated the entire procedure using the other leader rat to lay a trail to and from the left arm of the maze and five naive follower rats to test the efficacy of the trail the second leader had deposited.

We repeated the entire procedure for 7 consecutive days, alternating leader rats between days and testing five experimentally naive follower rats on each day.

Results and Discussion

On all 7 days (3 days on which a leader rat travelled to and from the left arm of the maze and 4 days on which it travelled to and from the

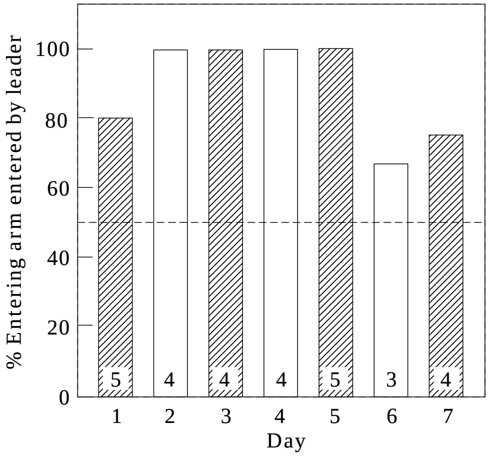

Figure 1. Percentage of follower rats entering the arm of the maze that their respective leader rats had entered on each of the seven trials of experiment 1. ▨: Leader rat entered right arm of maze; □: leader rat entered left arm of maze. Numbers inside histograms indicate the number of followers out of five entering an arm of the maze within 5 min after the start-box door was opened.

right arm of the maze), follower rats showed a preference for the arm of the maze which their leader rat had visited (sign test: $x=0$, $P<0.02$; Fig. 1). We concluded that leader rats travelling to and from a feeding site deposited residual cues that biased movement by conspecifics. It is also possible that follower rats deposited cues that added to the signal that their leader had initiated.

EXPERIMENT 2: DO RATS FOLLOW A SINGLE RAT TRAIL?

Although the results of experiment 1 provide compelling evidence that naive rats will follow trails deposited by their fellows, the methods used were rather unwieldy. In experiment 2, we established the adequacy of less time-consuming and expensive procedures for examining the effects of residual cues deposited by leader rats on the paths chosen by their followers under conditions where follower rats could not influence one another's behaviour.

Methods

Subjects

We used the same two leader rats in experiment 2 that we had used in experiment 1 and 12 experimentally naive, 42-day-old, female follower rats from the vivarium of the McMaster University Psychology Department.

Apparatus

We used the same apparatus as in experiment 1.

Procedure

Deposition of trails by leaders. We used similar procedures as in experiment 1, except that in experiment 2: (1) we permitted a leader rat to make only one round trip from start box to left or right arm of the maze and back before we removed her from the maze, and (2) we rewarded the leader with eight 45-mg food pellets in each food cup she encountered.

Testing followers. We used similar procedures to those in experiment 1, except that in experiment 2, we tested only a single follower rat with the trail deposited by each leader rat before we cleaned the floor of the apparatus.

Results and Discussion

Two of the 12 follower rats did not enter an arm of the maze within 5 min of our opening the start-box door, and, because they failed to choose between arms of the maze, we removed them from the experiment. Nine of the 10 follower rats that did enter an arm of the maze within 5 min of release from the start box entered the same arm of the maze that their leader had entered (binomial test: $x=1$, $P<0.02$). Thus, leader rats deposited sufficient amounts of residual material during a single trip to and from a feeding site to bias path selection by rats that came after them.

EXPERIMENT 3: ARE TRAILS LAID TO OR FROM FOOD?

In experiment 3, we investigated the conditions under which leader rats deposit residual cues that bias subsequent path choice by conspecifics.

Experiment 3 is presented as three studies. In the first and second, we determined whether leader rats: (study 1) deposited attractive trails on their way to food or (study 2) after they had left a feeding site. In a third study, we determined whether ingestion at a potential feeding site affected whether leader rats subsequently deposited a trail attractive to their followers.

Methods

Subjects

We used the same two leader rats as in experiment 1 and 39 experimentally naive female rats from the McMaster vivarium as followers.

Procedure

Study 1. The procedure was the same as that used in experiment 2, except that we removed the leader rat from the arm of the maze it entered as soon as it ate from the food cup located there. Thus, leader rats had the opportunity to deposit a trail as they moved from the start box of the apparatus to an arm of the maze, but had no opportunity to deposit a trail after they had eaten in an arm of the maze.

We habituated both leader rats to the new procedure for several days before we started study 1, and used 14 naive subjects as follower rats.

Study 2. The procedure here was the same as that used in experiment 2 except that on each trial of study 2, we placed the leader rat directly into an arm of the maze, 5 cm from and facing the food cup, let her eat the eight pellets she found there and then run to the start box.

We had habituated both leader rats to the new procedure for several days before we started the study, and we used 14 experimentally naive rats as followers.

Study 3. The procedure was the same as that used in experiment 2 except that a leader rat received no food reward in the food cup of the arm of the maze that it entered. We used 11 experimentally naive rats as followers, and we accustomed leader rats to a partial reward schedule in the maze for several days before starting the study.

Results and Discussion

Leader rats did not deposit trails attractive to followers either while running from the start box of the maze to a maze arm in which they ate (study 1, binomial test: $x=5$, NS) or while running from an arm of the maze to the start box after they failed to find food in that arm of the maze (study 3, binomial test: $x=5$, NS; Fig. 2).

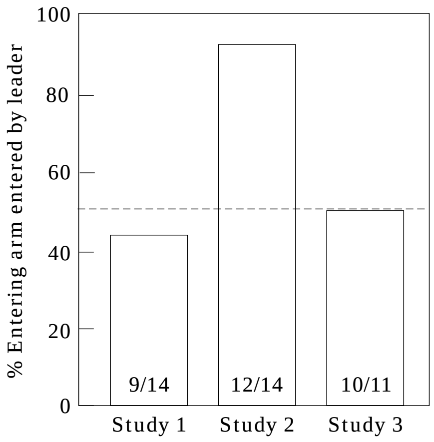

Figure 2. Percentage of follower rats entering the arm of the maze that their respective leader rats had entered in studies 1, 2, and 3 of experiment 3. The denominator of the fraction inside each histogram indicates the number of follower rats run in that study; the numerator indicates the number of followers entering an arm of the maze within 5 min after the start-box door was opened.

Leader rats did deposit attractive trails while returning to the start box after eating in an arm of the maze (study 2, binomial test: $x=1$, $P<0.01$; Fig. 2).

The results of experiment 3 are most parsimoniously described as indicating that, at least under the conditions of the present experiment, rats deposited trails attractive to their fellows only after leaving a location where they had eaten.

EXPERIMENT 4: DO AMOUNT OF FOOD AND REPEATED TRAIL USE AFFECT TRAIL ATTRACTIVENESS?

In experiment 4, we determined: (study 1) whether follower rats would respond differently to trails deposited by rats that had eaten relatively large amounts of food than to trails deposited by rats that had eaten relatively small amounts of food and (study 2) to trails laid down during a single passage by a leader rat than to trails laid down in the course of many passages by a leader rat.

Study 1. Before beginning this study, we habituated two new leader rats for several days to sometimes finding one food pellet and sometimes finding eight food pellets in each food cup they encountered.

To begin study 1, we closed the left arm of the maze, placed the leader rat trained to enter the right arm of the maze in the start box and opened the start-box door. The leader rat then ran to the food cup in the left arm of the maze, ate whatever pellets she found there and returned to the start box. We then removed that leader rat from the maze, opened the left arm of the maze and closed its right arm, placed the other leader rat in the start box, opened the start-box door and let the second leader rat run to the food cup at the end of the right arm, eat whatever pellets she found there and return to the start box.

On each trial, one of the two leader rats found eight pellets in the arm of the maze that she entered, and the other leader rat found only a single pellet in the arm of the maze that she entered. We counterbalanced across follower rats both the order in which we ran leaders to left and right arms of the maze and the order in which leader rats found one or eight pellets in the arm of the maze that they entered.

Study 2. The methods were the same as those of study 1 except that in study 2: (1) the same two leader rats each found four 45-mg food pellets in each food cup that they visited, and (2) each of nine follower rats chose between a trail deposited by a leader going once to an arm of the maze and the trail deposited by the other leader rat shuttling back and forth 10 times between the second arm of the maze and the start box. We counterbalanced across followers: (1) the order in which we allowed leader rats to deposit one or 10 trails and (2) whether the single trail and 10 trails were deposited by leader rats going to the left or right arms of the maze.

Results and Discussion

Study 1. Eight of 10 follower rats in study 1 entered an arm of the maze within 5 min after we opened the start-box door. Four of those eight rats entered the arm of the maze entered by the leader rat that had eaten eight pellets; four entered the arm of the maze entered by the leader rat that had eaten one pellet (binomial test: $x=4$, NS). The data provide no support for the hypothesis that the movement of follower rats is more strongly influenced by trails laid down by leader rats that have eaten a large amount of food than by trails deposited by those that have eaten a small amount of food.

Study 2. Seven of the nine follower rats in study 2 entered an arm of the maze within 5 min after the door of the start box was opened, and all seven of those follower rats entered the arm of the maze which a leader rat had traversed 10 times rather than the arm of the maze that a leader rat had traversed only once ($x=0$, $P<0.01$). Thus, the movements of follower rats are more strongly biased by a trail traversed several times by a leader rat than by a trail deposited by a leader rat during a single traverse.

EXPERIMENT 5: CAN RATS DETECT THE DIRECTION OF A TRAIL?

We conducted experiment 5 to determine whether follower rats would respond to the direction of movement of a leader rat either towards or away from food.

Methods

Subjects

The same two 49-day-old female rats served as leader rats in experiment 4 served as leader rats in this experiment. Eleven 42-day-old rats born and reared in the McMaster vivarium served as followers.

Apparatus

We used the same apparatus in the present experiment that we had used in experiments 1–4, but modified the apparatus to accommodate a guillotine door located at the junction between the alley and the arms of the T-maze. When this door was in place, the two arms of the maze formed a closed straight alley, and rats could not pass from the arms of the maze to the alley leading back to the start box.

Procedure

Training leaders. With the new guillotine door in place, we trained one leader rat, when placed in the left arm of the maze, to run to the food cup located at the end of the right arm of the maze, to eat, and then to run back to the food cup located at the end of the left arm of the maze. We trained the second leader rat, when placed in the right arm of the maze, to run to the food cup located at the end of the left arm of the maze, to eat, then to run back to the food cup in the left arm of the maze. Once both leader rats were running reliably in the maze and had become accustomed to intermittent reinforcement when they returned to their starting point, we were ready to test followers.

Testing followers. On a test day, we first placed the guillotine door at the junction between the alley and arms of the T-maze. We then placed a leader rat in one arm of the maze, allowed her to run to the end of the other arm of the maze, to eat and then to run back to her starting point (where she was not fed) before we removed her from the maze. We then removed the guillotine door from the junction between the alley and arms of the maze, placed a follower rat in the start box, opened the start-box door and allowed the follower 5 min to choose an arm of the maze to enter. As soon as the follower rat selected an arm of the maze, we removed her from the apparatus and then washed the apparatus floor.

In all, we observed six follower rats in the apparatus after a leader had run from the left arm of the maze to the right and eaten before returning to its starting point and five follower rats whose leader ran in the opposite direction.

Results and Discussion

Ten of the 11 follower rats selected an arm of the maze to enter within 5 min after we opened the start-box door. Four of these 10 followers entered the arm of the maze where their leader had eaten, and six entered the other arm of the maze. There was no indication that the trails deposited by leader rats caused their followers to move along a trail towards food rather than away from it. The trails deposited by leader rats do not appear to be polarized.

GENERAL DISCUSSION

The results of the five experiments described above each provide evidence consistent with the view that recently fed rats departing from a feeding site deposit residual trails that are attractive to conspecifics. The data thus establish a sixth way in which a Norway rat that has been successful in finding food might facilitate the later discovery and exploitation of that food by its fellows.

The observed redundancy in mechanisms of social foraging in Norway rats suggests that the need to locate ephemeral or widely scattered potential food sources has been important in the evolution of their social behaviour. Similarly, other social, central-place foraging species have evolved redundant mechanisms for communicating with conspecifics about the availability, nature or location of foods (e.g. honey bees or ants: von Frisch 1967; Wilson 1971). Indeed, the trail laying shown by successful rat foragers as they departed from feeding sites in the present experiments is at least superficially similar to the trail laying shown by ants that, when returning from a feeding site to their nests, deposit chemical trails that lead nestmates to foods that successful foragers discovered (Wilson 1971; Hölldobler & Wilson 1990).

Unfortunately, we do not yet know as much about the composition of the trails that rats deposit after feeding as we do about analogous trails deposited by ants, the source and nature of which are fairly well understood (Wilson 1971; Hölldobler & Wilson 1990).

The trails deposited by rats after they leave a feeding site could come from any of a number of different sources. Possibly particles of food falling from the paws or fur of rats were accidentally deposited on the substrate by leader rats as they travelled back to the start box from a feeding site; perhaps leader rats deposited scent marks from sebaceous glands on the palmar and plantar soles of their feet or by rubbing their bodies on the substrate as they moved through the maze (reviewed in Brown 1985); perhaps, after eating, leader rats excreted urine containing attractive scents (Reiff 1956; Richards & Stevens 1974).

Observation of the behaviour of leader rats in the maze and of the maze itself after rats had traversed it provided helpful clues but no conclusive evidence as to the nature of the attractants that leader rats deposited there. We detected no overt scent-marking behaviour by leader rats as we observed them transverse the maze on hundreds of occasions. When we examined the floor of the maze after a leader rat had crossed it, we often found a scattering of transparent, lightly tinted droplets or dried residues of some liquid on the surfaces that the rats had traversed. We suspect but cannot confirm that these droplets and residues were rat urine.

In future studies of the nature of the attractive trails deposited by rats after they leave a feeding site, our working hypothesis will be that some component of urine excreted by rats after feeding can affect the choice of path made by conspecifics as they move through unfamiliar environments.

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