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Socially acquired information reduces Norway rats' latencies to find food

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Abstract. Experiments have demonstrated that socially acquired information influences both where Norway rats, *Rattus norvegicus*, look for food and what foods they eat. The present studies were undertaken to determine whether rats could also use information acquired from conspecifics to determine when food had become available. Naive rats introduced either into colonies that had been trained to come to a feeding site when food was made available there or into colonies lacking such training. The former naive animals began to feed on introduced food with significantly shorter latencies than did the latter. Naive rats tended to leave a shelter they shared with others and travel to a feeding site after interacting at the shelter with a returning successful forager, but not after interacting there with a returning unsuccessful forager. Furthermore, naive rats that had been trained to eat a food, but not naive rats trained to avoid eating the same food, left shelter and went to a feeding site after interacting in the shelter with a returning forager that had eaten the food that naive rats had been trained either to eat or to avoid. All results were consistent with the view that naive colony members could learn that food had become available at a familiar feeding site by interacting with colony members that had recently eaten there.

After a recently fed Norway rat, *Rattus norvegicus*, (a demonstrator) interacts with a naive conspecific (an observer rat), the observer increases its relative intake of whatever food its demonstrator ate (Galef & Wigmore 1983; Galef 1991; Galef & Whiskin 1992). Thus, one Norway rat can learn from another what foods to eat.

Norway rats can also use information acquired from conspecifics to discover where food is to be found. For example, as a rat moves away from a feeding site, it deposits a scent trail that biases the movement of other rats encountering that trail and increases the probability that they will travel to the feeding site at its end (Galef & Buckley 1996; see also Galef & Heiber 1976; Galef & Beck 1985).

It seems reasonable to suppose that, as has been suggested for other species that forage socially from a central site (e.g. Weatherhead 1987; deGroot 1998, but see Mock et al. 1988), socially acquired information might increase the efficiency with which Norway rats exploit foods that are ephemeral and patchy in distribution (Ward & Zahavi 1973; Bertram 1978; Wittenberger & Hunt 1985; Allchin 1992; Galef & Whiskin 1994; Richner & Heeb 1995). If so, one would expect rats to be able to learn from their fellows not only where to go to find food and what foods to look for, but also when food had become available.

The present series of experiments was undertaken to determine whether Norway rats could, in fact, use interaction with conspecifics to reduce their latency to find a food that had reappeared at a location where it had previously been available.

EXPERIMENT 1: TRAINED AND UNTRAINED DEMONSTRATORS

In experiment 1, we compared the latencies of naive rats to find food after we reintroduced them into one of two kinds of colonies: (1) colonies whose members we had trained to come to a feeding site as soon as food was placed there and (2) colonies whose members lacked such training. On the hypothesis that naive rats can use interactions with conspecifics to learn when a food has become available, we expected that naive rats that we introduced into trained colonies would begin

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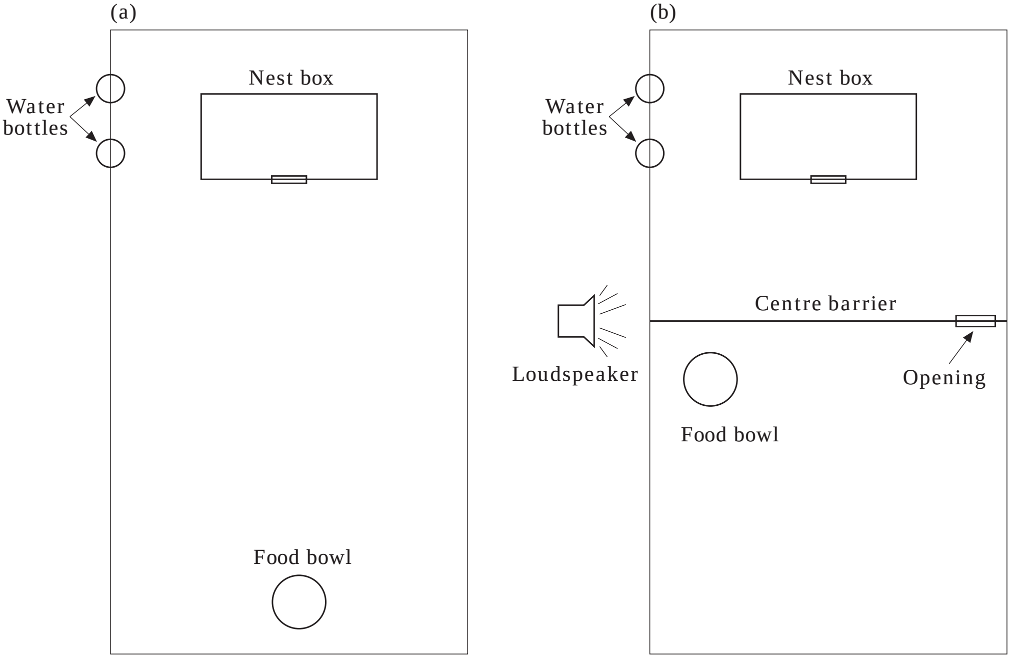

Figure 1. Overhead schematic of enclosures used in (a) experiment 1 and (b) experiments 2–4.

to exploit a reintroduced food sooner than would naive rats that we introduced into untrained colonies.

Methods

Subjects

Seventy-two 42-day-old female, Long Evans rats born in the vivarium of the McMaster University Psychology Department (Hamilton, Ontario) to breeding stock acquired from Charles River Canada (St Constant, Quebec) served as subjects that we maintained throughout the experiment on a 12:12 h light:dark cycle with light onset at 0800 hours.

We randomly assigned each subject to one of 24 trios of rats, then randomly assigned one rat within each trio to serve as a ‘focal subject’ and the other two rats in that trio to serve as ‘demonstrators’. Finally, we randomly assigned half the trios to the experimental condition and half to the control condition described in Procedure.

Apparatus

During the experiment, we housed each trio of subjects in an enclosure measuring 2 × 1 × 0.3 m that we had constructed of sheet metal, angle iron and hardware cloth (Fig. 1a). We covered the galvanized, sheet-metal floors of enclosures with a thin layer of wood-chip bedding, and placed two water bottles and a single, wooden nest-box (measuring 30 × 15 × 15 cm) with a single entrance in each enclosure.

We presented food in each enclosure in a ceramic bowl that we always placed in the same location (Fig. 1a). The bowl measured 15 cm in diameter and was large enough to permit several young female rats to feed simultaneously without either getting in one another’s way or interacting aggressively.

Procedure

Day 1. At noon on day 1 of the experiment, we shaved the posterior of the focal subject in each trio and marked her with red ink so that when we reviewed videotapes we could easily distinguish the focal subject from the two demonstrators in her group. We then placed both demonstrators from each trio we had assigned to the experimental condition in an enclosure that had no food present at the feeding site. At the same time, we placed each pair of demonstrators in trios that we had assigned to the control condition in an enclosure where we had already placed a food bowl containing powdered Purina Rodent Laboratory Chow #5001 (Ralston-Purina, Woodstock, Ontario).

Days 2–4. From 1100 to 1200 hours on each of the next 3 days, we placed a food bowl containing powdered Purina chow at the feeding site in each of the 12 enclosures containing a pair of demonstrators assigned to the experimental condition. For the same 3 days, we left demonstrators in all 12 trios assigned to the control condition with ad libitum access to powdered Purina chow at the feeding sites in their respective enclosures. Thus, we trained demonstrators assigned to the experimental condition to come to the feeding station when we placed food there; demonstrators that we had assigned to the control condition did not receive such training.

During days 2, 3 and half of day 4, we kept the focal member of each trio in her home cage and gave her ad libitum access to pellets of Purina Rodent Laboratory Chow #5001.

To ensure that focal subjects learned both where food could be found in an enclosure and what food was available there, at noon on day 4, we placed the focal member of each trio in the enclosure with her demonstrators and left all 24 trios to feed for 24 h from a bowl of powdered Purina chow that remained at the feeding station.

Day 5. At noon on day 5, we removed the food bowls from all 24 enclosures.

Day 6. At 1100 hours on day 6 (the test day), we placed a bowl of powdered Purina chow at the feeding station in each of the 24 enclosures and videotaped the vicinity of the food bowl for the next 60 min.

When reviewing videotapes, we recorded the latency to begin eating of both the focal subject and the first demonstrator to eat in each trio.

Results and Discussion

As we had expected, demonstrator rats assigned to the experimental condition began to feed sooner after we introduced a food bowl into their respective enclosures on the test day ($\text{median} = 0.44$ min) than did demonstrator rats assigned to the control condition ($\text{median} \geqslant 60.0$ min; Mann–Whitney *U*-test: $U = 0$, $P < 0.0001$). Clearly, we had succeeded in training demonstrators in experimental trios to come to the feeding site when we placed food there.

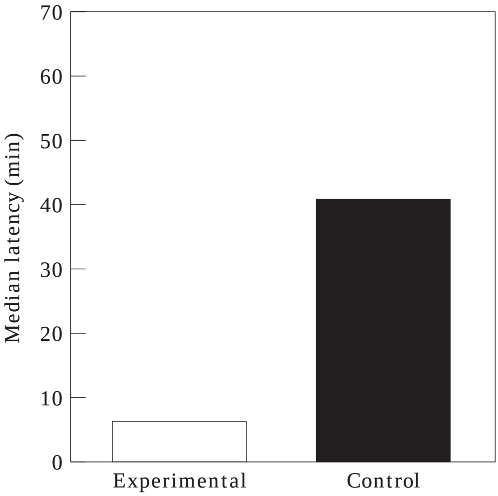

Figure 2. Median latencies to eat of focal subjects assigned to experimental and control conditions in experiment 1.

As we expected on the hypothesis that naive rats could use interactions with fellow colony members to determine when food had become available, focal subjects in trios assigned to the experimental condition found food far more rapidly after we had placed it at the feeding site than did focal subjects in trios assigned to the control condition ($U = 12$, $P < 0.01$; Fig. 2). Apparently focal animals in trios assigned to the experimental condition were recruited to the feeding site by their respective demonstrators.

EXPERIMENT 2: EXCLUDING LOCAL ENHANCEMENT

There are trivial explanations for the finding in experiment 1 that focal members of trios assigned to the experimental condition found food more rapidly than did focal members of trios assigned to the control condition. For example, the former animals may simply have seen or heard their respective demonstrators eating and joined them at the food bowl.

Although such local enhancement of feeding would be expected to occur whenever demonstrators were eating within sight or sound of the focal members of their respective trios, local enhancement of feeding by rats and other animals has been demonstrated many times before and is, therefore, not particularly worthy of note.

We undertook experiment 2 to determine whether the reduced latency to reach a newly available food, exhibited by focal subjects in the experimental group in experiment 1, would still be observed if local enhancement by demonstrators of focal subjects' approach to feeding sites was not possible.

Methods

Subjects

Forty-eight 42-day-old female Long Evans rats from the vivarium of the McMaster University Psychology Department served as members of 16 trios each containing a randomly selected focal subject and two demonstrators. We randomly assigned half the trios to the experimental condition and half to the control condition described in Procedure.

Apparatus

We modified the apparatus used in experiment 1 in four ways to prevent focal subjects in or near a nestbox from responding directly to demonstrators at a feeding site (Fig. 1b). First, we rotated the nestbox 180°, so that its entrance faced away from the feeding site. Second, we interposed a galvanized sheet-metal barrier with a single opening at one end between the nestbox and feeding station. Third, we moved the feeding station so that it was not visible from the vicinity of the nestbox. Last, we placed a loudspeaker driven by a white-noise generator near the barrier that separated the nest site from the feeding area and adjusted the intensity of the white noise so that normal speech in the experimental room was effectively masked.

The combination of an opaque barrier (that blocked any visual or ultrasonic contact between animals at the nestbox and feeding station) and a source of white noise (that severely impeded any sonic contact between animals at a distance from one another) prevented direct recruitment of focal animals from nestbox to feeding station.

Procedure

The procedure of experiment 2 was identical to that of experiment 1, except that we conducted experiment 2 with (1) the nestbox rotated and the barrier in place between nestbox and feeding station and (2) the white-noise generator activated.

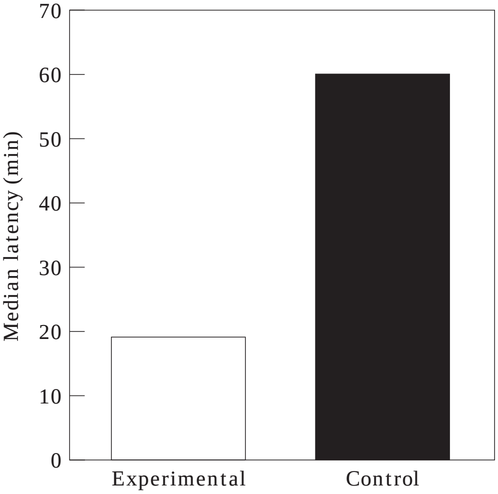

Figure 3. Median latencies to eat of focal subjects assigned to experimental and control conditions in experiment 2.

Results and Discussion

As in experiment 1, on the test day, demonstrators assigned to the experimental condition reached the food bowl significantly more rapidly (median = 0.95 min) than did demonstrators assigned to the control condition (median > 60.0 min; $U = 0$, $P < 0.0001$).

Also as in experiment 1, on the test day, focal members of trios assigned to the experimental condition began to feed far sooner than did focal members of trios assigned to the control condition ($U = 8$, $P < 0.01$; Fig. 3).

The results of experiment 2 indicate that something other than simple local enhancement recruited focal subjects assigned to the experimental condition to the feeding station when food was reintroduced there on the test day.

EXPERIMENT 3: FOOD OR NO FOOD AT THE FEEDING SITE

In experiments 1 and 2, as would be the case in field observation of a colony of wild Norway rats, all we observed of the behaviour of our subjects was their comings and goings near their respective feeding sites. In experiment 3, we observed trio members throughout the enclosures in which they were held so as to be able to generate hypotheses as to how demonstrator rats were recruiting focal subjects to feeding sites.

Also, in experiment 3, we were interested in determining whether focal subjects were sensitive to the success of foragers returning to the nest site when deciding whether to leave the nest site and travel to the feeding site.

Methods

Subjects

Ninety-nine 42-day-old female Long Evans rats from the vivarium of the Psychology Department of McMaster University served as subjects that we randomly assigned to 33 trios. We also randomly assigned focal subjects and demonstrators within trios, then assigned trios to the No Food ($N=14$ trios) and Food ($N=19$ trios) conditions described in Procedure.

Apparatus

In experiment 3, we used the same apparatus we had used in experiment 2 (Fig. 1b), except that we replaced the wooden lids of nestboxes with lids of transparent Plexiglas that allowed us to observe behaviour inside nestboxes as well as in open areas of enclosures. We also changed the focal length of the lens on our television camera so that we could monitor the behaviour of subjects throughout enclosures, not just in the vicinity of feeding sites.

Procedure

We treated the 19 trios assigned to the Food condition in the present experiment exactly as we had treated trios assigned to the experimental condition in experiment 2, and the 14 trios assigned to the No Food condition exactly as we treated subjects assigned to the Food condition, except from 1100 to 1200 hours on the test day (day 6). When we placed a bowl containing powdered Purina chow at the feeding site in each of the 19 enclosures containing trios assigned to the Food condition, we placed an empty bowl at the feeding site in each of the 14 enclosures containing trios assigned to the No Food condition.

Because there was no food available to focal subjects assigned to the No Food condition, we used the latency between introduction of a bowl into an enclosure and the time when subjects first touched that bowl (rather than the latency between introduction of a bowl and first feeding by subjects) as our dependent variable.

We also recorded occurrence of any interactions between demonstrators and focal subjects that took place away from the feeding site. We considered a demonstrator and focal subject to have interacted away from the feeding site if their noses came within one head length of each other while they were on the far side of the partition from the feeding site (Fig. 1b).

Results and Discussion

Observations of trios assigned to the Food condition

When we introduced a food bowl into an enclosure, focal subjects were always either in or near the nestbox. They most often appeared to be asleep inside the shelter. At the time we introduced food into an enclosure, demonstrators were sometimes in the nestbox with the focal subject and sometimes waiting at the feeding site.

After demonstrators started to feed, they would make excursions back to the nestbox, where they often interacted with focal subjects.

Five of the 19 focal subjects in trios assigned to the Food condition, left the nestbox and reached the food bowl before either of their respective demonstrators had returned to the nestbox from the feeding site. Four of these five focal subjects reached the food bowl within 2 min of introduction of the food bowl into their respective enclosures. These focal subjects appeared to have left the nestbox in response to the departure of their demonstrators, when the demonstrators left the nestbox to search for food. The last of the five focal subjects that left its nestbox and began to eat before interacting with a demonstrator did not reach the food bowl for 15 min after its demonstrators had left the nestbox and started to feed.

There was considerable variability in the latencies of the remaining 14 focal subjects assigned to the Food condition to reach the food bowl after it was introduced into their respective enclosures (Fig. 4a). This variability was not reduced noticeably by examining focal subjects' latencies to contact the food bowl after their respective

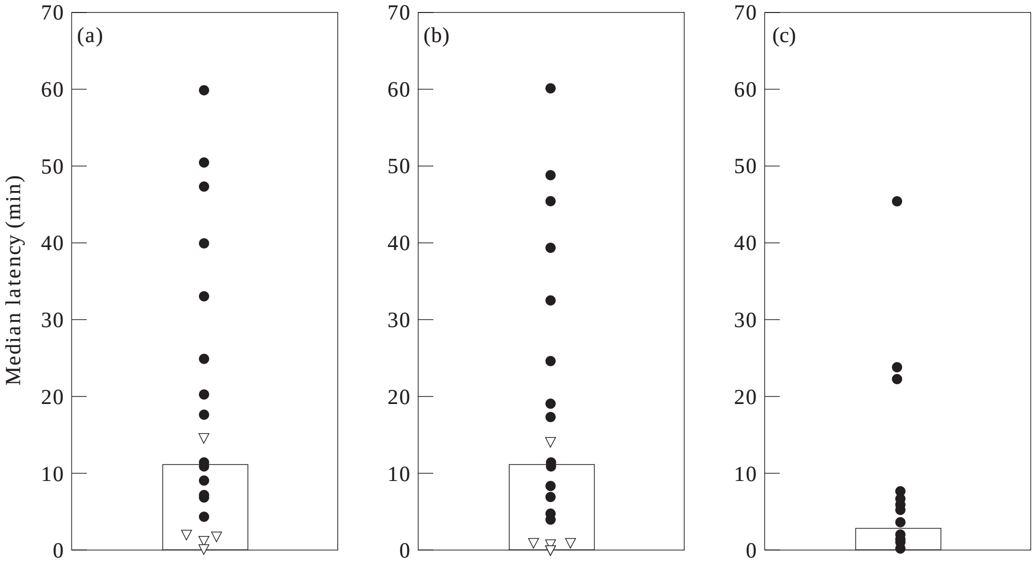

Figure 4. Median latencies of focal subjects assigned to the Food condition in experiment 3. (a) To reach food, (b) to reach food after their respective demonstrators had begun to eat and (c) to reach food after interacting for the first time with a demonstrator that had eaten. (▽) Latencies of individual focal subjects that reached food before they had interacted with a demonstrator; (●) latencies of individual focal subjects that, before reaching the food bowl, interacted with a demonstrator that had eaten.

demonstrators had done so (Fig. 4b). Thus, these 14 focal subjects did not appear to leave the nestbox and go to the feeding site in response to their demonstrators' initial departure from the nestbox at about the time when food was introduced into enclosures.

On the other hand, when we examined the latencies of these 14 focal subjects to contact the food bowl after their first interaction with a demonstrator returning from the food bowl, much of the variance in their latencies to contact the food bowl disappeared (Fig. 4c). Thus, these 14 focal subjects appeared to leave the nestbox and travel to the feeding site in response to one of the periodic visits made to the nestbox by their respective demonstrators.

As indicated below, comparison of the behaviour of focal subjects assigned to trios in Food and No Food conditions was also consistent with the hypothesis that focal subjects assigned to the Food condition were responding to interaction with demonstrators returning from feeding by leaving the nestbox and going to the feeding site in their respective enclosures.

Comparison of the behaviour of subjects assigned to Food and No Food conditions

None of the 14 focal subjects in trios assigned to the No Food condition arrived at the feeding station before one of its demonstrators had returned from the feeding site to the nestbox; as noted above, five of the 19 focal subjects in trios assigned to the Food condition did so. This difference in the frequency with which focal subjects assigned to the two conditions went to the feeding site before interacting with a demonstrator was a result of all demonstrators in the No Food condition returning to the nestbox and interacting with the focal member of their respective trios immediately after they discovered the empty food bowl. Thus, there was essentially no opportunity for focal animals assigned to the No Food group to go to the feeding site before interacting with a demonstrator.

Focal subjects in the No Food condition took significantly longer than did subjects in the Food condition to reach food bowls after we had placed them in enclosures on the test day ($U=60$, $P<0.01$; Fig. 5a). Seven of the 14 focal subjects in

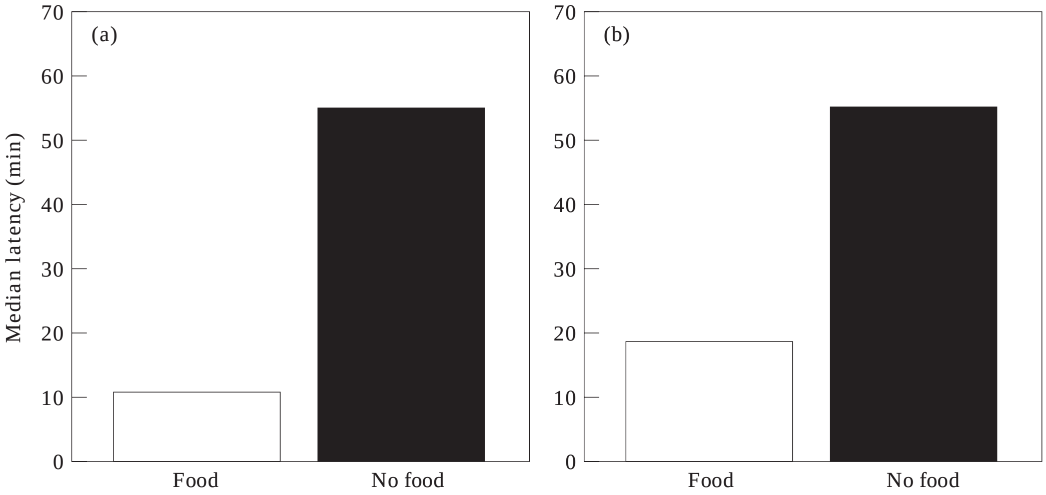

Figure 5. Median latencies to reach food bowls of focal subjects assigned to Food and No Food conditions in experiment 3. (a) Data for all focal subjects, (b) data for those focal subjects that reached a food bowl after interacting with a demonstrator.

the No Food condition never reached the food bowl despite interacting with demonstrators significantly more often ($\bar{X} \pm \mathrm{SE} = 7.6 \pm 1.1$ times) than did focal subjects in the Food condition before they first reached the food bowl (1.6 ± 0.4 times; Welch's approximate t: $t_{16} = 5.12$, $P < 0.0001$). Focal subjects obviously responded differently to demonstrators that either had or had not found food at their respective feeding sites.

In the present experiment, we were particularly interested in differences in the responses of focal subjects to interaction with demonstrators that had or had not eaten at their respective feeding sites before returning to the nestbox. Only those 14 focal subjects in trios assigned to the Food condition that interacted with a demonstrator before leaving the nestbox provided information on the response of focal animals to demonstrators that had eaten.

The 14 focal subjects in trios assigned to the Food condition that did not go to the feeding site before interacting with a demonstrator had significantly shorter latencies to reach the food bowl than did the 14 focal subjects in trios assigned to the No Food condition ($U = 55$, $P < 0.05$; Fig. 5b).

This difference in the median latencies of focal subjects assigned to the No Food and Food conditions to reach the food bowl during the test period suggests that focal subjects may have determined whether a returning demonstrator had succeeded in finding food and left their harbourage sites to seek food only after interacting with a successful forager. However, demonstrators in trios assigned to the No Food condition moved from the feeding site to the nestbox far more frequently than did demonstrators in trios assigned to the Food condition. Consequently, differences either in the frequency of nestbox visits or in other aspects of the behaviour of demonstrators in trios assigned to Food and No Food conditions may have been responsible for the difference we observed in the latencies to reach feeding sites of focal subjects in trios assigned to experimental and control conditions. We undertook experiment 4 to determine whether the foraging success of demonstrators could influence the latency to seek food shown by focal subjects with which demonstrators interacted.

EXPERIMENT 4: SAFE AND TOXIC FOOD

As noted above, one explanation of the difference in response of focal subjects to fed and unfed demonstrators is that focal subjects left their nestboxes and sought food only in response to interaction with demonstrators that had actually eaten.

The present experiment was based on the assumption that potential foods an animal has learned to avoid eating because they are toxic are no longer considered by that animal to be food. If rats do not consider substances to which they have learned an aversion to be food, and if focal subjects are recruited to a feeding site by interaction only with demonstrators that have eaten, then whether focal subjects have learned an aversion to the food that demonstrators ate should have a profound effect on the effectiveness of demonstrators in recruiting focal subjects to a feeding site.

If, on the other hand, some difference in the behaviour of fed and unfed demonstrators (rather than whether they ate food) was responsible for differences in the latencies to reach a feeding site of focal animals in Food and No Food groups in experiment 3, then focal subjects' perceptions as to the toxicity or safety of food eaten by their respective demonstrators should not affect focal subjects' latencies to leave shelter and move to a feeding site.

Methods

Subjects

Ninety-three 42-day-old female Long Evans rats from the vivarium of the Psychology Department of McMaster University served as subjects that we assigned to 31 trios. We randomly assigned trios to the Aversion ($N=16$ trios) and No Aversion ($N=15$) conditions described in Procedure and randomly assigned subjects to serve as focal subjects and demonstrators within trios.

Apparatus

We used the same apparatus that we had used in experiments 2 and 3.

Procedures

Training focal animals in the Aversion groups. To induce aversions in focal subjects assigned to trios in the Aversion condition without placing them on a feeding schedule, we put each focal subject alone in a hanging cage with a small bowl containing a known amount of a palatable casein and corn-starch based diet, diet NPT (Normal Protein Test Diet, Teklad Diets, Madison, Wisconsin, Catalogue number 170590). We weighed the food bowl once each hour until each focal subject had eaten over 2.0 g of diet NPT. Once a subject had done so, we removed the bowl containing diet NPT from that subject's cage and injected her intraperitoneally with 2% of body weight, 1% wt/volume lithium chloride solution.

Training focal animals in the No Aversion group. We treated focal subjects in trios assigned to the No Aversion condition exactly as we had treated focal subjects assigned to trios in the Aversion condition except that (1) we injected subjects assigned to the No Aversion condition with lithium-chloride solution 24 h before we placed a weighed bowl of diet NPT in their individual cages, and (2) we did not inject subjects assigned to the No Aversion condition after they ate 2 g of diet NPT.

*Testing.*The remainder of the procedure of the present experiment was identical to that used with trios assigned to the Food condition in experiment 3 except that, on the test day (day 6), we placed a bowl containing diet NPT, rather than a bowl containing powdered Purina chow, at the feeding station in the enclosure containing each trio.

Results and Discussion

As we had expected, given the experimental design, there was no difference in the median latencies of demonstrators in trios assigned to Aversion and No Aversion groups to first reach the food bowl ($U=116$, NS).

We also found no difference in the median latencies to reach the feeding area of focal subjects assigned to Aversion and No Aversion conditions that left the nestbox and reached the food bowl before interacting with a demonstrator ($U=17$, NS; Fig. 6b).

As we had expected, however, on the hypotheses that (1) focal subjects that have learned that a food is toxic no longer consider that substance to be food and (2) focal subjects use information acquired from their demonstrators to determine whether the demonstrators have recently eaten food, the median latency to first visit the feeding site of focal subjects assigned to the Aversion condition that did not visit the feeding site until after they interacted with demonstrators ($N=10$) was significantly longer than that of comparable

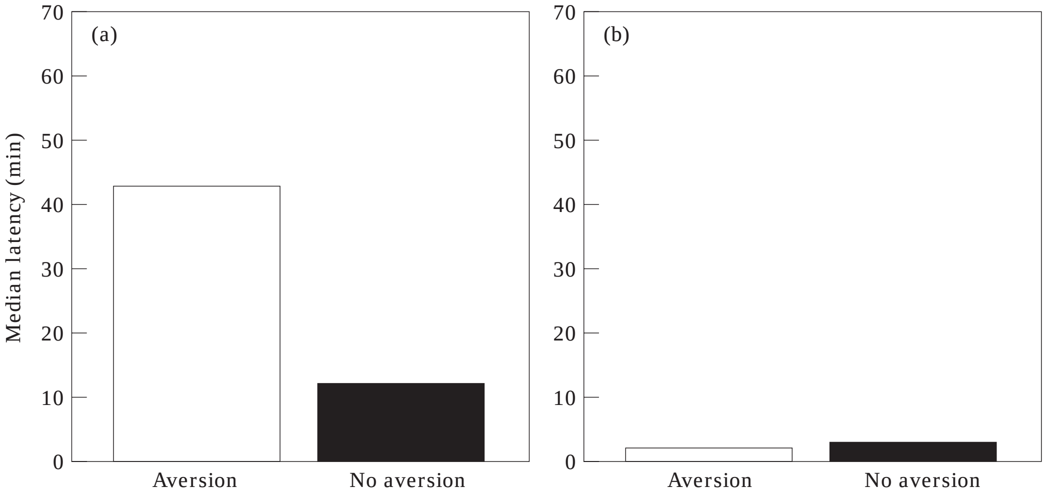

Figure 6. Median latencies to eat of focal subjects assigned to Aversion and No Aversion conditions in experiment 4. (a) Focal subjects that reached a food bowl after interacting with a demonstrator that had eaten, (b) focal subjects that reached a food bowl before interacting with a demonstrator that had eaten.

focal subjects assigned to the No Aversion group ($N=8$; $U=10$, $P<0.001$; Fig. 6a).

GENERAL DISCUSSION

The results of these experiments indicate that naive Norway rats can increase the efficiency with which they find a reintroduced food by using information acquired from conspecifics that have discovered and eaten that food; naive individuals leave shelter and seek food shortly after interacting with a forager returning to shelter between bouts of feeding.

Focal subjects appeared to be sensitive to the success of returning foragers in finding food; they began to exploit a reintroduced food more rapidly after interacting with a returning forager that had eaten food than after interacting with either an unsuccessful forager or a successful forager that had eaten a substance that the focal subjects had learned to avoid eating.

Taken together, the results of the four experiments reported above demonstrate that Norway rats can use socially acquired information to increase the efficiency with which they begin to exploit foods that are intermittently available at fixed locations. Socially acquired information allows Norway rats to determine not only what and where to eat, but when to eat as well.

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REFERENCES

Allchin, D. 1992. Simulation and analysis of information-center foraging. *Behaviour*, **122,** 288–305.

Bertram, B. C. R. 1978. Living in groups: predators and prey. In: *Behavioural Ecology* (Ed. by J. R. Krebs & N. B. Davies), pp. 64–96. Sunderland, Massachusetts: Sinauer.

Galef, B. G., Jr. 1991. Information centres of Norway rats: sites for information exchange and information parasitism. *Anim. Behav.*, **41,** 295–302.

Galef, B. G., Jr & Beck, M. 1985. Attractive and aversive marking of toxic and safe foods by Norway rats. *Behavl neural Biol.*, **43,** 298–310.

Galef, B. G., Jr & Buckley, L. L. 1996. Use of foraging trails by Norway rats. *Anim. Behav.*, **51,** 765–771.

Galef, B. G., Jr & Heiber, L. 1976. The role of residual olfactory cues in the determination of feeding site selection and exploration patterns of domestic rats. *J. comp. physiol. Psychol.*, **90,** 727–739.

Galef, B. G., Jr & Whiskin, E. E. 1992. Social transmission of information about multiflavoured foods. *Anim. Learn. Behav.*, **20,** 56–62.

Galef, B. G., Jr & Whiskin, E. E. 1994. Passage of time reduces effects of familiarity on social learning: functional implications. *Anim. Behav.*, **48,** 1057–1062.

Galef, B. G., Jr & Wigmore, S. W. 1983. Transfer of information concerning distant foods: a laboratory investigation of the 'information centre' hypothesis. *Anim. Behav.*, **31,** 748–758.

deGroot, P. 1980. Information transfer in a socially roosting weaver bird, *Quelea quelea* (Plocinae): an experimental study. *Anim. Behav.*, **28,** 1249–1254.

Mock, D. W., Lamey, T. C. & Thompson, D. B. A. 1988. Falsifiability and the information centre hypothesis. *Ornis Scand.*, **19,** 231–248.

Richner, H. & Heeb, P. 1995. Is the information centre hypothesis a flop? *Adv. Study Behav.*, **24,** 1–46.

Ward, P. & Zahavi, A. 1973. The importance of certain assemblages of birds as 'information-centres' for food finding. *Ibis*, **115,** 517–534.

Weatherhead, P. 1987. Field tests of information transfer in communally roosting birds. *Anim. Behav.*, **35,** 614–615.

Wittenberger, J. F. & Hunt, G. L. 1985. The adaptive significance of coloniality in birds. In: *Avian Biology, Vol. VIII* (Ed. by D. S. Farner, J. R. King & K. C. Parkes), pp. 2–78. New York: Academic Press.