Winning Isn’t Everything: Rats Need Only Food Deprivation and Not Food Reward to Efficiently Traverse a Radial Arm Maze

WILLIAM TIMBERLAKE AND WESLEY WHITE

Indiana University

The present study examined the assumption that immediate food reward is the critical determinant of efficient performance on the radial maze. Food-deprived and nondeprived rats were run on a large-platformed, 8-arm radial maze that was either baited or unbaited. Food-deprived rats that were rewarded entered significantly more novel arms in their first eight choices than expected by chance, consistently ran to the ends of chosen arms, and increasingly chose adjacent arms over trials. Food-deprived rats that were unrewarded behaved in much the same way. In contrast, rats that were nondeprived and unrewarded did not choose novel arms at above chance levels, infrequently ran to the ends of chosen arms, and did not develop a consistent response strategy. Explanations of the development of organized behavior based on reinforcement, win-shift tendencies, or spontaneous alternation do not account for these results. Rats appear to have foraging strategies based on preorganized stimulus sensitivities and response dispositions that are readily engaged by food deprivation and result in efficient traversal of a radial maze even in the absence of food reward.

Since its reintroduction by Olton and Samuelson (1976), the radial maze has been the primary apparatus for examining the spatial memory of rats. The maze consists of a central, circular “hub” from which equally-spaced arms radiate. In the typical procedure, after a food pellet is placed at the end of each arm, a rat is placed on the center platform and allowed to traverse the maze until it has found and eaten all the pellets. After brief experience with an 8-arm maze, rats collect food pellets very efficiently. Often within 20 trials rats enter between 7.5 and 8.0 novel arms in their first eight choices (Olton & Samuelson, 1976).

This research was supported by NSF Grant BNS 84-11445 and NIMH Grant MH37892. The order of authorship was determined by a coin flip. We thank Sue Thomason for her critical assistance. Address correspondence to W. Timberlake, Psychology Department, Indiana University, Bloomington, IN 47405.
As pointed out by Olton, Handelmann, and Walker (1981), classic reinforcement theory (Hull, 1943; Skinner, 1938) predicts that a response followed by food should be immediately strengthened. Thus, in a radial arm maze the choice of a particular baited arm should perseverate to the detriment of other available responses, the precise form of the perseveration depending on the rate of dissipation of any choice-specific inhibition. However, the local behavior of rats on the radial maze, and in foraging tasks in general, usually is not consistent with perseveration. Rats go to alternative food sources much more readily than they return to sources recently visited, even if the latter are not depleted (Olton, Walker, Gage, & Johnson, 1977). Thus, though some local perseverative effect of reward may occur (e.g., Gaffen & Davies, 1981), the maze behavior of a rat clearly is structured by considerably more than the tendency to immediately repeat a food-reinforced response.

Olton et al. (1981), and Olton and Schlosberg (1978) argued that underlying the local behavior of rats in a radial maze is a win-shift foraging strategy. Once a rat encounters a prey item in a particular place, it is much more likely to immediately explore alternative areas than to return to that place. This win-shift strategy in rats is presumably a tactic that has been selected during evolutionary time to take advantage of their niche-characteristic spatial and temporal distribution of food.

While acknowledging the importance of Olton's insight, we argue here that the win-shift account does not go far enough in recognizing characteristics of organized foraging that are independent of the local discovery of food. Much research has shown that behavior relevant to food-finding can be systematic and efficient even in the absence of food. For example, chimpanzees fit sticks together, reach with sticks, and stack and climb on boxes with increasing coordination in the absence of food incentives (Schiller, 1952). Rodents persist in manipulatory responses that do not produce food (Fowler, 1965). Rats placed in a straight alley without any food show most of the changes in performance over trials shown by food-rewarded rats (Timberlake, 1983). Similarly, the performance of rats run without food reward on a 6-arm Dashiel maze is not distinguishable from the performance of rats running for reward (FitzGerald, Isler, Rosenberg, Oettinger, & Battig, 1985). Finally, both rewarded and unrewarded rats tend to alternate choices in a T-maze (e.g., Dember & Fowler, 1958).

These observations raise the possibility that efficient performance by rats in the radial maze is based on evolved search strategies readily engaged by food deprivation but expressed in the absence of local food reward. Such search strategies presumably depend on an appetitive structure of stimulus sensitivities and response predispositions that have been selected to promote efficient foraging under typical ecological circumstances (Timberlake & Lucas, 1989).
The present study tested the hypothesis that evolved search strategies underlying efficient traversal of the radial maze by rats do not require local food reward for their expression. The present study compared performance on the radial maze in three groups of rats: food-deprived and food-rewarded, food-deprived and unrewarded, and neither food-deprived nor food-rewarded. Comparison of the two deprived groups should reveal the extent to which efficient spatial search depends on food reward. Comparison of the two unrewarded groups should reveal the contribution of a deprivation schedule to efficient spatial search. Comparison of the two unrewarded groups should also suggest whether the tendency to choose novel arms depends primarily on the tendency toward spontaneous alternation of arms. If unrewarded deprived and nondeprived subjects traverse the radial maze with different degrees of efficiency, the performance difference cannot be ascribed solely to spontaneous alternation, because spontaneous alternation is reported to be little affected by deprivation (e.g., Dember & Fowler, 1958). Finally, the radial maze used in the present study had a large central platform. Rats receiving food on a maze with a large platform have been shown to select a greater percentage of neighboring arms than counterparts on a maze with a small platform (Yoerg & Kamil, 1982). Thus, the present experiment may clarify the relative contribution of deprivation and reward in engendering response patterning.

METHOD

Subjects

The subjects were 26 experimentally naive female albino rats bred at the Indiana University colony. The subjects were reared in pairs, but they were housed individually and handled during the 10 days prior to their first trial on the maze. Rats were handled for several minutes each day by repeatedly picking each subject up from a table top and putting it back down, and by weighing it. Twenty of these subjects were also food deprived to 85% of their free-feeding body weights during this time. Rats were permitted free access to water in their home cages and were fed standard laboratory rat chow to maintain their body weights. The food-deprived rats were 90 to 120 days old at the start of the study. The six undeprived rats were 90 to 150 days old. Colony lights came on at 6:30 AM and went off at 6:30 PM.

Materials

Subjects were run on an elevated 8-arm radial maze. The platform and arms were raised 67 cm above the floor. The round central platform was 86 cm in diameter. The platform had 17 equally spaced slots into which arms could be inserted. Arms were placed in eight of these slots so that
they were approximately evenly distributed. The arms were 10-cm wide and 70-cm long. Each arm was enclosed by sidewalls. The right sidewall was 3-cm high. The first 32 cm of the left sidewall was 12-cm high and the rest was 3-cm high. A 2.5-cm diameter depression (a food cup) was drilled into the end of each arm. The maze was painted grey and was housed in a quiet, unadorned, well-lighted room approximately 3-m × 2.5-m × 2.5-m high. A door was in one corner of the room, and the experimenter set in another corner recording data at a small desk.

**Procedure**

Ten deprived subjects were assigned to a rewarded group (D–R) and 10 deprived subjects were assigned to an unrewarded group (D–U). Two rats were subsequently dropped from each deprived group because they entered fewer than eight arms on five consecutive trials. One of the six nondeprived and unrewarded subjects (N–U) was dropped for the same reason. The subjects in the deprived–rewarded group were given 10 to 15 45-mg Bio Serv pellets in their home cages, along with their standard maintenance ration, on each of the 2 days prior to their first trial on the maze. Subjects in the other two groups did not receive Bio Serv pellets. Before all trials, the maze was cleaned with a deodorant solvent and disinfectant. For the deprived–rewarded group, a single 45-mg Bio Serv pellet was placed in the food cup at the end of each arm. The maze was never baited for the other groups.

All subjects were brought individually from the colony to the maze room. They were placed on the center of the platform, oriented toward the experimenter, and were allowed to move through the maze until they had made 12 choices or until 10 min elapsed, whichever came first. At the end of a trial, subjects were immediately returned to the colony where they were given their daily food ration about 5 min after their trial. Subsequent research has shown that this immediate feeding procedure was not responsible for the choice patterns obtained. Rats were run 5 days a week at approximately 4 PM. All subjects were run one trial per day for 24 trials. During a trial, the experimenter recorded the arms a rat entered, the order in which choices were made, and whether the rat completed the arm. A rat entered an arm when it placed 4 feet in an alley simultaneously. A rat traversed an arm when its entire body was a minimum of 32 cm from the edge of the platform.

**Data Concentration Rules**

Subjects showed considerable variation in the consistency with which they ran. Two subjects in the deprived–rewarded condition, four subjects in the deprived–unrewarded condition, and one subject in the nondeprived–unrewarded condition failed to make at least eight choices within 10 min on approximately half the trials. These trials with varying numbers
of choices, though distributed fairly evenly across days, made it difficult to compare the average number of novel arms chosen to the number expected on the basis of chance. To minimize this difficulty, we focused on trials on which the animals made at least eight choices by combining data within 3-day blocks using the following rules.

If a subject made at least eight choices in all three trials within a block, then the median number of novel choices was used in the calculation of the group average. If a subject made at least eight choices in two trials, then the average number of novel choices made in these trials was used. If a subject made at least eight choices in only one trial, then the number of novel choices in that trial was used. Finally, if a subject failed to make at least eight choices in all three trials within a block, then the average of the preceding and subsequent blocks was used in the calculation of the group average. This last rule was employed only 4 of 64 possible times for the D-R group, 6 of 64 times for the D-U group, and 3 of 40 times for the N-U group. Averages for the other measures were calculated using the same rules, except that all sessions with at least two choices were used.

RESULTS

Figure 1 shows the average number of novel arms that rats in each group entered in their first eight choices, computed as outlined above for each block of three trials. The bars extending down from each point represent the lower halves of 95% confidence intervals. If rats chose arms randomly, they would enter, on the average, 5.3 novel arms in

![Figure 1](image-url)

**Fig. 1.** Average novel choices as a function of three-trial blocks for food-deprived and maze-rewarded (D-R), deprived and unrewarded (D-U), and nondeprived and unrewarded (N-U) subjects. Averages were calculated on the basis of the first eight choices. Lines extending vertically from plotted points show lower halves of 95% confidence intervals. The first, second, and third lines at a given block are confidence intervals for the D-R, D-U, and N-U groups, respectively. The horizontal line is chance performance.
their first eight choices. The 95% confidence intervals show that subjects in deprived–rewarded (D–R) and deprived–unrewarded (D–U) conditions selected novel arms at above chance levels beginning with the very first trial block. The nondeprived–unrewarded (N–U) subjects showed above chance performance on only the second trial block.

A repeated ANOVA in which the three groups served as the between-factor and blocks of trials served as the within-factor revealed a significant difference in choice performance due to groups, $F(2, 18) = 11.83$, $p < .05$. A difference in performance due to blocks just failed to be significant, $F(7, 14) = 2.06$, $p = .053$, and there was no groups $\times$ blocks interaction, $F(14, 126) = 1.53$, $p > .10$. When choice scores in blocks 7 and 8 were combined to represent asymptotic performance, an ANOVA showed that the choice performance of the groups was significantly different, $F(2, 18) = 17.50$, $p < .05$. Tukey tests indicated that the D–R group made more novel choices than the D–U and N–U groups, and the D–U group made more novel choices than the N–U group.

Figure 2 depicts, for successive blocks of three trials, the average percentage of occasions upon which animals chose adjacent arms up to their eighth selection. A groups $\times$ blocks repeated ANOVA indicated a significant effect due to groups, $F(2, 18) = 5.53$, $p < .05$, and blocks, $F(7, 14) = 7.38$, $p < .05$, and a significant groups $\times$ blocks interaction, $F(14, 126) = 2.30$, $p < .05$. Tests for simple main effects of blocks were significant for D–R, $F(7, 126) = 6.46$, $p < .05$; D–U, $F(7, 126) = 3.06$, $p < .05$; and N–U groups, $F(4, 126) = 4.71$, $p < .05$. In the two deprived groups, animals were more likely to choose an adjacent arm as experience
with the maze increased. In the N–U group the change in patterning was more variable and not systematic.

Comparison of Fig. 1 and 2 showed that deprived subjects were selecting novel arms at above chance levels before they selected adjacent arms on a high percentage of occasions. This is especially clear in the unrewarded group. Thus a memory for spatial locations selected, rather than a simple response algorithm, probably mediated the high performance levels. When scores in blocks 7 and 8 were combined to represent asymptotic performance, an ANOVA showed that the percentage of adjacent arms chosen by groups differed, \( F(2, 18) = 4.58, p < .05 \). Tukey tests showed that only the D–R and N–U groups differed at asymptote on this measure.

Finally, Fig. 3 shows the average percentage of their first eight choices on which animals went to the ends of chosen arms. A groups \( \times \) blocks repeated ANOVA indicated a significant effect due to groups, \( F(2, 18) = 21.20, p < .05 \); blocks, \( F(7, 14) = 4.21, p < .05 \); and a significant groups \( \times \) blocks interaction, \( F(14, 126) = 3.43, p < .05 \). Tests for simple main effects of blocks detected a significant difference in only the N–U group, \( F(4, 126) = 11.75, p < .05 \). The deprived subjects traversed a high percentage of arms from the outset. When scores in blocks 7 and 8 were combined to represent asymptotic performance, an ANOVA showed that the percentage of traverses made by groups of subjects differed, \( F(2, 18) = 19.14, p < .05 \). Tukey tests showed that percentage of traverses made by D–R and D–U groups differed from the percentage of traverses made by N–U subjects, but not from one another.

![Fig. 3. Average percentage of chosen arms traversed as a function of three-trial blocks for food-deprived and maze-rewarded (D–R), deprived and unrewarded (D–U), and non-deprived and unrewarded (N–U) subjects. Averages were calculated on the basis of up to eight choices.](image)
DISCUSSION

Whether food-rewarded or not, deprived rats traversed the radial arm maze efficiently. Deprived rats chose novel arms at a level above chance, completely traversed the great majority of arms chosen, and increased their choice of neighboring arms across sessions. In other words, their search behavior was efficient, exhaustive, and became increasingly systematic over trials. In contrast, nondeprived rats did not choose novel arms above chance, did not traverse the majority of arms chosen, and did not systematically increase their choice of neighboring arms across sessions.

The similarity of behavior in the rewarded and unrewarded groups of deprived rats indicates that neither the strengthening effects of reinforcement nor win-shift foraging strategies provide the fundamental basis for maze behavior. The major determinants of efficient maze search are clearly independent of local food reward. However, several differences between the behavior of rewarded and unrewarded rats suggest that reward slightly facilitated the efficiency of search behavior. More rewarded rats consistently made at least eight choices (six vs. four animals). Rewarded animals also patterned more and chose slightly but significantly more novel arms at asymptote.

The greater choice of novel arms at asymptote by the rewarded group may have been related to the increased response patterning and may represent an overall strategy of optimizing intake. The direction of this effect, though, appears to contradict the results of Gaffen and Davies (1981) who found that under some conditions food reward increased the tendency to persist in rather than to alternate choices. Perhaps this difference occurred because Gaffen and Davies (1981) replenished food in arms after the initial choice assessment, introducing a different optimal strategy for the second choice assessment. However, it is not clear why the difference obtained by Gaffen and Davies (1981) did not occur for water or why it disappeared over trials for food.

The marked difference between the behavior of deprived and nondeprived rats suggests that spontaneous alternation is also not an adequate account of these results. Though some data indicate that deprivation enhances overall locomotor behavior (e.g., Berlyne, 1960), there is no evidence that alternation is reduced to chance levels in the absence of deprivation. Because of the frequent failure of nondeprived subjects to complete arms in the present experiment, it might be argued that their inferior choice performance was due to inadequate coding of the arms (Mazmanian & Roberts, 1983). But the rank order correlation between average novel choices and number of arms traversed for the nondeprived rats was only .20, indicating little relation between complete traversal and probability of choosing a novel arm.
A general but potentially more inclusive account of our results is provided by the behavior systems approach recently reviewed by Timberlake and Lucas (1989). In this view, stimulus circumstances sufficiently similar to those of the animal's selection environment engage and support organized appetitive behavior. This behavior is based on an underlying appetitive structure of preorganized perceptual–motor modules and motivational propensities evolved to serve a specific functional end, such as finding spatially distributed food.

A key characteristic of appetitive behavior is that although it may be modified by immediate payoffs, such payoffs frequently are not necessary for its development. Thus, though the strategies displayed by the rat in efficient traversal of the radial maze presumably evolved based on their effectiveness in finding food, they do not require actually finding food to be expressed in a form that changes with experience. These strategies do, though, appear to be more readily engaged and expressed by food-deprived rats in the present experiment.

Schiller (1952) argued that researchers frequently do not conceive of complex responses as native to animals because animals are not studied prior to training. The present experiment extends this argument to the acquisition of foraging behavior by rats on a radial maze. Behavioral changes due to food reward have not been adequately distinguished from changes due to simple repeated exposure to the apparatus (see also Timberlake, 1983). Increased likelihood of finding food is probably an ultimate (evolutionary) reason that rats systematically traverse a maze, but food is not required as a proximate cause to produce systematic search. In fact, rats will continue to check daily a location in a maze even though it contains a food previously associated with poisoning (Melcer & Timberlake, 1985).

Such a separation of proximate and ultimate control makes sense for an animal, like the rat, that frequently cannot anticipate where and when food will be found. Considerable unrewarded locomotion is often required to find food. Rats that persistently explored their environments efficiently in spite of momentary food scarcity were probably more likely in the long run to ingest an adequate diet, survive, and reproduce. A rat whose food-seeking behavior depended exclusively upon proximate food reward for organization and persistence would not survive very long.

The degree of response patterning in the present study supported the report of Yoerg and Kamil (1982) that choice of neighboring arms in a radial maze increased with the size of the central platform. The greater degree of patterning with a larger platform can be attributed in part to the tendency of rats to remain near the edge of open areas. Such a tendency is difficult to express in a small-platformed maze because there is little space between arms and a much sharper turn is required to return to the edge of the platform in time to choose the adjacent arm.
Though response patterning on the maze does not entail complex memory for high levels of choice, several observations indicate that memory is a key mediating variable. In the present study rats chose novel arms at above-chance levels well before they began to pattern, especially in the unrewarded group. So it is clear that initial differences among the groups were based on memory and not solely on a simple response algorithm. Once patterning became predominant it was not possible to determine whether high choice performance continued to be mediated by memory or by a response algorithm alone. However, other research has shown that rats retain a memory for visited locations even when they pattern (Foreman, 1985).

Finally, the spatial memory of rats run in baited mazes has been shown to be remarkably persistent (Beatty & Shavalia, 1980), and resistant to within-session retroactive (Maki, Brokofsky, & Berg, 1979; Roberts, 1981, 1984) and proactive interference (Roberts, 1984). Whether these properties of memory also characterize the selection of unbaited arms as shown in this study remains to be seen.

REFERENCES


Received July 17, 1989
Revised November 8, 1989