Maze patrolling by rats with and without food reward

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The effects of food reward on rats' behavior in radial and Dashiell tunnel mazes were examined in two experiments. In the first, with animals at ad-lib body weights, food reward reduced speed of movement at the food locations, but did not affect the patterns of movement in either maze. Exploratory efficiency in the Dashiell maze was unaffected by food reward, and spontaneous patrolling of the radial maze by the nonrewarded animals was comparable to the behavior, reported by others, of rats running for food reward on elevated eight-arm mazes. In the second experiment, with subjects maintained at 80% of ad-lib body weights, there was some evidence for "win-stay" learning: food-rewarded rats in the Dashiell maze were relatively more active near the food locations than were the nonrewarded animals, and more rewarded than nonrewarded rats revisited all food locations in the radial maze. Nonetheless, exploratory efficiency in the Dashiell maze was unaffected by food reward, as was patrolling efficiency in the radial maze, which was again comparable to that of rats on elevated mazes. The similarity in behavior of rewarded and nonrewarded animals in these mazes implies that the major determinant of their behavior, whether or not food reward is provided, is a spontaneous tendency to avoid places recently visited.

Early studies with Y- and T-mazes (Berlyne, 1960; Dember & Fowler, 1958; Fowler, 1965) observed that the tendency of the rat to alternate between goal arms in mazes is independent of whether the rat is satiated or hungry or whether the choices are food rewarded or not. More recently, radial arm mazes have become popular as a tool in behavioral research. In such mazes, the rat is trained to collect food placed at the arm ends; its task is to avoid reentering arms it has previously visited. Rats become extremely proficient at this task—in an eight-arm radial maze, they typically make an average of more than seven choices before reentering an arm (Olton & Samuelson, 1976). We have previously described spontaneous nonrewarded patrolling by rats in complex asymmetrical tunnel mazes (Bättig, 1983; Bättig & Schlatter, 1979; Nil & Bättig, 1981). The first purpose of the present study was to describe spontaneous radial-maze patrolling, and to compare it to the behavior of rats running for food.

The theoretical question we address in this study is why rats running for food reward in radial mazes perform so proficiently. This was initially attributed to their preference for "win-shift" behavior, which is interpreted as a species-specific foraging strategy (Olton, Handelmann, & Walker, 1981; Olton & Schlosberg, 1978). More recent studies, however, have emphasized the fact that the rat has a strong tendency to follow a shift strategy, whether or not it is food rewarded for doing so (Gaffan & Davies, 1981, 1982; Gaffan, Hansel, & Smith, 1983; Haig, Rawlins, Olton, Mead, & Taylor, 1983). Gaffan and Davies (1981, 1982) could find no evidence for enhanced arm alternation produced by food reward (win-

shift) in radial and T-mazes, and concluded that the maze behavior of rats is adequately accounted for by a combination of the principle of spontaneous alternation and the principle of associative memory, whereby the rat prefers places associated with food to those associated with no food (win-stay; Gaffan & Davies, 1981). Unfortunately, it is difficult in T- and radial mazes to dissociate patrolling for food (win-shift) from spontaneous patrolling, since the same path must be taken both to collect all food and to completely explore the maze (see Gaffan & Davies, 1981, p. 296). In a Dashiell-type maze, by contrast, there are multiple routes from any given start to any given goal location; the rat can visit food-rewarded areas of the maze without ambulating through areas never associated with food. If rats do follow a win-shift strategy, we would expect food reward to increase activity in the nonrewarded areas of the Dashiell maze. If they follow a win-stay strategy, however, food reward should reduce activity in nonrewarded areas of the maze. The second goal of this study was thus to seek evidence, in radial and Dashiell mazes, for win-shift and/or win-stay behavior.

In Experiment 1, we tested rats at ad-lib body weight, in order to measure normal spontaneous behavior. The incentive value of food was increased in Experiment 2 by food depriving the subjects to 80% of ad-lib body weight.

EXPERIMENT 1

Method

Subjects. Thirty experimentally naive 3-month-old Wistar-derived Roman high-avoidance (RHA/Verh) male rats from the Institute's breeding colony were used. Their weights ranged from 200 to 300 g at the start of the experiment. The rats were group housed (10 per cage) in Macrolon cages in a temperature- and humidity-controlled

room (23°C, 50% relative humidity). They were on a 12-h light/dark cycle and were tested during the dark phase. Food and water were available ad lib until the day prior to experimentation. On this day, and for all subsequent experimental days, food became available for only 4h/day, beginning after the last rat in a given cage had been tested. Water was continuously available. On this feeding schedule the rats gained weight slowly during the experiment.

Apparatus. An external view of the maze and its ground plan are shown in Figure 1. The enclosed alleys were 8 cm wide and 15 cm high. Movement of the animal through the maze was measured by infrared beams 4 cm above the floor; the 42 locations monitored are shown in Figure 1b. Sensor outputs were numbered and timed in a buffer and transferred to a PDP 11/34 minicomputer, which reconstructed the animal's movements in the maze. For statistical analysis, the data were shipped to a mainframe computer installation. The Dashiell configuration could be converted to a six-

Figure 1. (a) External view of the maze apparatus; (b) Ground plan of the maze, showing the activity sensor positions (circled) and the food locations (arrows); (c) Dashiell configuration and radial maze configuration (produced by inserting barriers into the Dashiell maze). Note that the food locations in the Dashiell maze correspond to the ends of the arms in the radial maze.

arm radially symmetrical maze by the insertion of barriers, as shown in Figure 1b and 1c. Within each arm was a choice point, leading on the left to a short blind alley, and on the right to the angled main center through which the rat was placed into the maze. The ceiling and walls formed a single unit, hinged to the wall of the room, which was raised from the floor for removal of the animal at the end of the session.
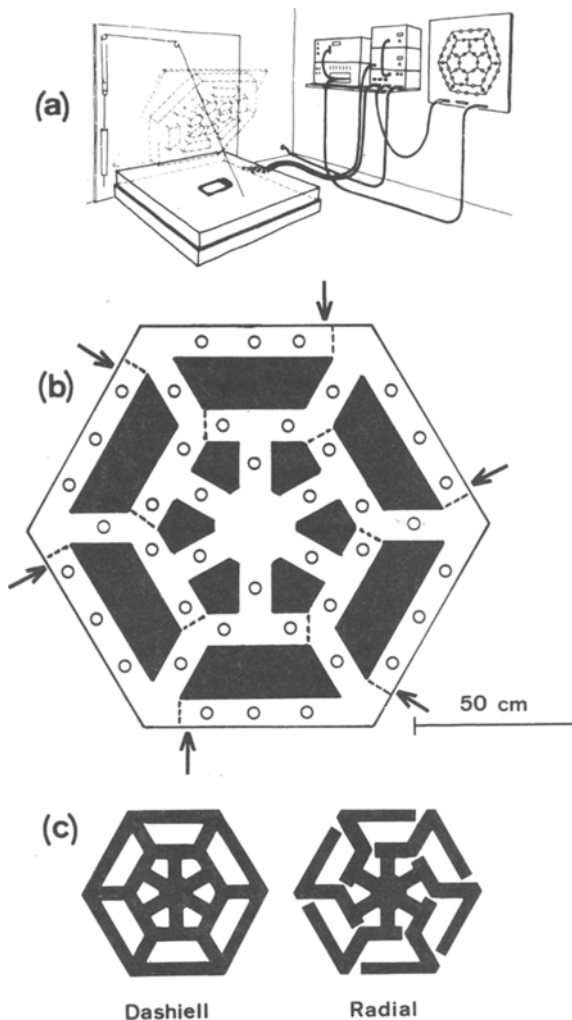
Procedure. The rats were divided randomly into two groups of 15 animals each. Subjects were given one daily 4.5-min session on 12 consecutive days. Because we were concerned about possible carryover effects from the radial to the Dashiell configuration, the Dashiell maze test was carried out first. On Days 1-6, the animals were tested in the Dashiell configuration, and on Days 7-12, in the six-arm radial configuration. For the food-rewarded group, one 45-mg Noyes pellet was placed at each of six locations in the outer corners of the maze (arrows in Figure 1b), corresponding to the arm ends in the radial configuration. The nonrewarded group never received food in the maze. At the beginning of a session, the rat was placed into the maze through the door in the maze center. After 4.5 min, the animal was removed by raising the maze, and any feces and urine were removed from the floor with a damp cloth. The order of testing within groups remained the same throughout the experiment, but the order of testing the two groups was alternated each day.

Behavioral measures and statistics. The variables used to describe behavior were as follows:

Dashiell: (1) Time to criterion: time in seconds to reach all six food locations, or, for animals that failed to reach all locations, total trial duration. (The term "food location" is also used for the nonrewarded group, for which there was no food at these locations.) (2) Explored area to criterion: number of different photocells interrupted to reach all six food locations, or for those animals that failed to reach all food locations, area covered during the entire trial (theoretical minimum 21, maximum 42, see Figure 1). (3) Activity to criterion: total number of photocell interruptions to reach all six food locations, or to the end of the trial. To exclude activity counts due to tail flicks, a given photocell had to be interrupted for at least 75 msec to be counted. (4) Activity distribution to criterion: percentage of activity counts occurring in the outer hexagonal runway and radial alleys of the maze until all six food locations were reached, or until trial end, whichever came first.

Radial: (1) Time to criterion: time in seconds to reach the midpoints of all six arms (defined as the cells in the outer radial runways). This criterion, rather than "all food locations visited," was used in all analyses because a number of animals, particularly nonrewarded animals in Experiment 2, entered all arms but turned around and left before reaching the ends (see Table 2). (2) Number of blind alley entries to criterion: Just after the entry point of each arm was a left/right choice, leading to a short blind alley or to the main goal arm. The number of entries into the six blind alleys were measured until all arms had been visited, or until trial end. (3) Choice stereotypy to criterion: percent frequency of the most frequent turn category in the choices until all arms were visited, or until trial end. This was calculated as $(x-c)/(1-c)*100$, where x = relative frequency of the most frequent turn category (-2, -1, 0, 1, 2, 3) and c = chance probability = 1/number of possible turn directions = 1/6. This formula was taken from Olton and Samuelson (1976), who used it to adjust the probability of a correct choice for chance. Its value can range from 0 (equal distribution of all turn directions between two anticlockwise and three clockwise) to 100 (all turns the same). (4) Number of repetitions to criterion: the number of repetitive arm visits occurring until all arms were visited, or total number of repetitions during the trial if criterion was not reached.

Except where noted otherwise, statistical analysis was by repeated measures ANOVA (BMDP program 2V; Dixon, 1983). Where appropriate, individual comparisons were made by t test. A significance level of $p < .05$ was adopted in all analyses.

Table 1
Number of Rats in Experiment 1 Reaching Criterion (All Food Locations) on Each Test Day

|	Dashiell						Radial					
Group	Day 1	Day 2	Day 3	Day 4	Day 5	Day 6	Day 1	Day 2	Day 3	Day 4	Day 5	Day 6
Food-rewarded	15	15	13	15	15	14	12	11	15	13	14	14
							(13)	(13)	(15)	(14)	(15)	(15)
Nonrewarded	15	15	15	15	15	13	12	14	13	15	14	13
							(14)	(15)	(14)	(15)	(15)	(15)

Note—Numbers in brackets refer to the number of rats reaching criterion (middle of all arms) in the radial maze.

Results

In the Dashiell maze, most, but not all, animals visited the six food locations during each test session. The numbers reaching criterion on each test day are given in Table 1. In the radial maze, several animals that failed to visit all food locations did enter all arms, but turned around and left before reaching the ends. In this experiment, the number of animals entering all arms was not significantly greater than the number reaching all food locations on any test day (by McNemar test; Siegel, 1956) (See Table 1).

Dashiell maze. Figure 2 shows mean values for time, area explored, activity, and activity distribution to criterion on each day of the experiment. There were significant session effects for all four variables [$Fs(5,140) > 2.9$], but no main effect of food reward and no significant reward × session interaction. Both groups were significantly more active in the outer part of the maze on Day 1 than on Day 6, by related t test. The only other significant difference between Day 1 and Day 6 was an increase in area explored to criterion in the nonrewarded group. This indicates that the food-rewarded rats did not learn to go straight from one food location to the next. Theoretically, a score of 21 different sensor activations would suffice to reach all the food locations (i.e., by running from the center of the maze to and around the outer hexagonal runway; see Figure 1). In fact, rather than decreasing, mean area explored to criterion in the rewarded group varied from about 26 on the first day to about 33 on the sixth test day. The proportion of activity in the outer part of the maze decreased significantly in both groups (related t tests), from about 70% on Day 1 to about 60% on Day 6. This phenomenon has previously been described as a "loss of centrifugal tendency" (Bättig & Schlatter, 1979; Nil & Bättig, 1981), and in the present experiment was not affected by the presence of food reward.

We also measured overall efficiency of movement in the maze, independent of behavior to criterion, by measuring the number of sensor activations to visit 6, 12, 18, 24, 30, 36, and 42 different sensors for the first time (see Nil & Bättig, 1981). Only 1 animal from each group interrupted all 42 sensors in the first test session, so data for this criterion and day are not shown; sample size for this criterion in all subsequent sessions was at least 8 per group. As shown in Figure 3, these scores suggest improvement in exploratory efficiency over the six test sessions for both groups. This was confirmed by repeated measures ANOVA on activity count to interrupt 36 differ-
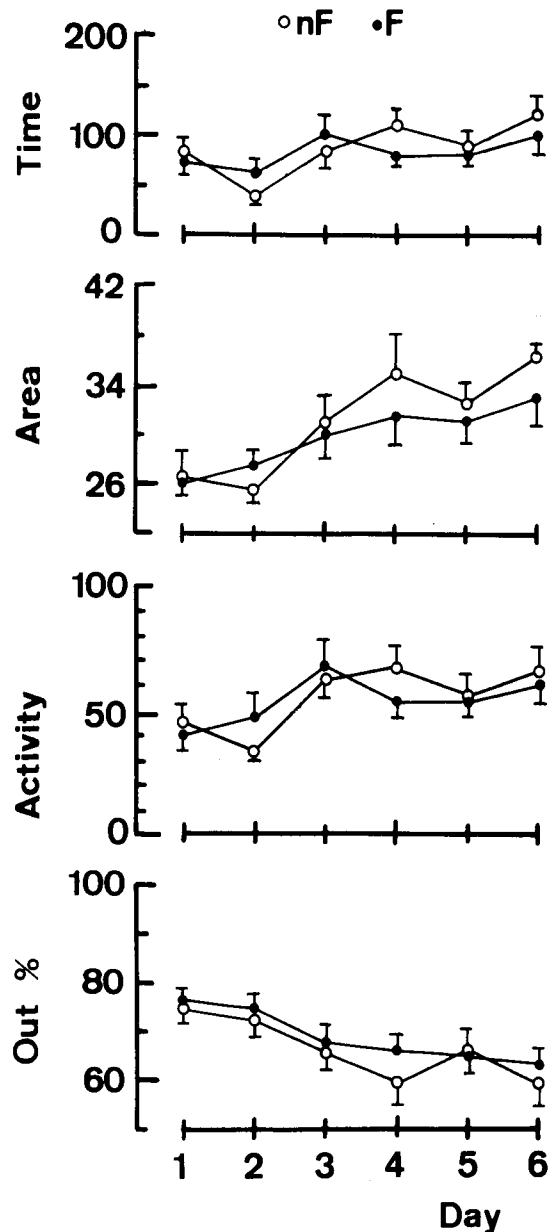
Figure 2. Behavior of food-rewarded (filled circles) and nonrewarded (open circles) groups to criterion (all food locations visited) in the Dashiell maze in Experiment 1 (animals at ad-lib body weights). From top to bottom: time in seconds to criterion; explored area, in terms of the number of different sensors activated; activity (number of sensor activations); and activity distribution (measured as percent activity in the outer part of the maze) in each of the six consecutive daily tests. (All values expressed as means ± SEM.)
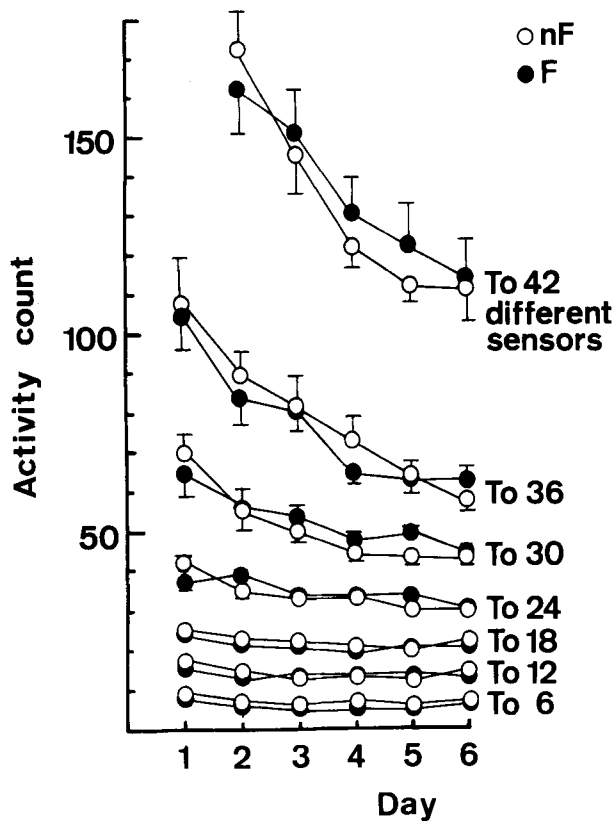
Figure 3. Exploratory efficiency of food-rewarded (F) and non-rewarded (nF) groups in the Dashiell maze in Experiment 1 (animals at ad-lib body weights); decreasing activity count over days to interrupt 24 and more different sensors indicates latent learning (see text for details). Values represent mean scores ± SEM.

in time to criterion; the rewarded group took longer overall to visit the food locations than the nonrewarded group [group F(1,28)=14.6]. This may have been due simply to the time spent eating the food pellets. We analyzed the transition times between adjacent sensors in all parts of the maze, and found significantly longer times for the food-rewarded group, but only for the food locations, as in the Dashiell maze. Both rewarded and nonrewarded groups were significantly faster to criterion on Day 6 than on Day 1, and made significantly fewer blind alley entries. Neither choice stereotypy nor number of repetitions
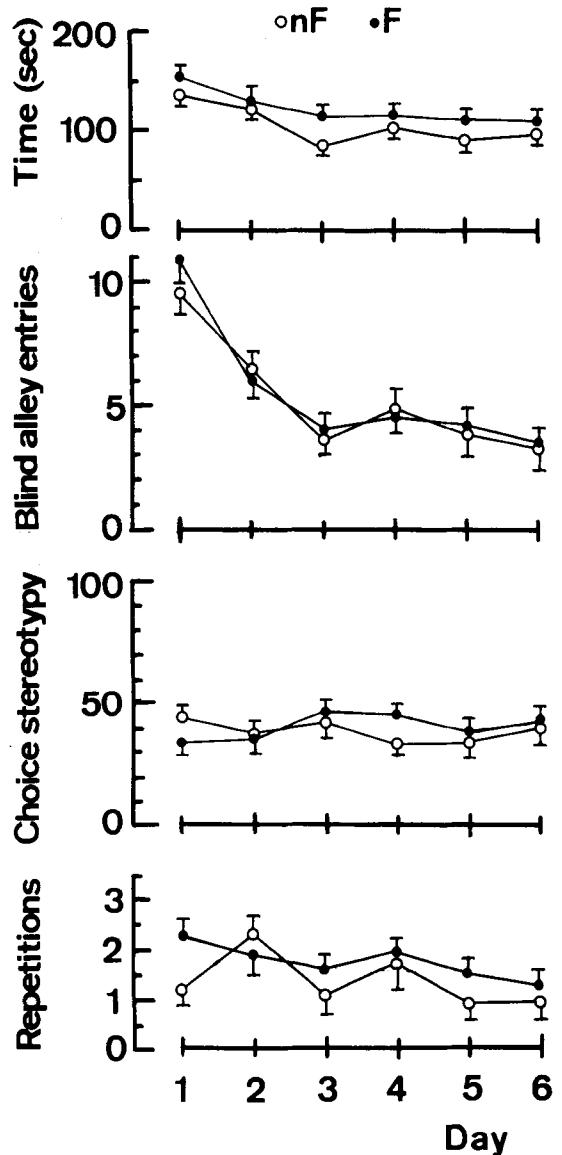

ent sensors, showing a significant sessions effect [F(5,140)=19.5], but no main or interaction effects of food reward. These data indicate that latent learning occurred (described by Bättig & Schlatter, 1979; Nil & Bättig, 1981), resulting in the rats' moving less redundantly over days through the Dashiell maze, and that this process was not affected by the presence of food.

Total activity in the Dashiell maze (i.e., total number of sensor activations during each 4.5-min trial) did not differ between the two groups over the 6 test days; in both groups, mean activity increased on Days 2 and 3, and then returned to baseline levels on Days 4-6 [session F(5,140)=6.4].

The only significant intergroup difference was obtained with an analysis of the transition times between sensors at the food locations. These were overall significantly longer in the rewarded than in the nonrewarded group [mean 3.1 vs. 2.7 sec, group F(1,28)=8.6]. There were no intergroup differences in transition times at the other loci (i.e., those loci not directly at the food locations).

Radial maze. Figure 4 shows, for each test session, mean scores for (from top to bottom) time, number of blind alley entries, choice stereotypy, and number of repetitive arm visits to criterion. The only significant difference between the two groups in the radial maze was

Figure 4. Behavior of food-rewarded (filled cirlces) and non-rewarded (open circles) groups to criterion (all arms visited) in the radial maze in Experiment 1 (animals at ad-lib body weights). From top to bottom: time in seconds to criterion; number of blind alley entries; choice stereotypy, measured as percent frequency of the most frequently occuring turn direction (see Method, Behavioral Measures section); and number of repetitive arm visits. All values are expressed as means ± SEM.

changed signficantly over days, and neither was affected by food reward.

In order to see how closely spontaneous radial maze patrolling in this six-arm tunnel maze resembed the behavior reported by others in eight-arm elevated mazes, we analyzed behavior in terms of three frequently reported measures of radial maze performance. The results are shown in Figure 5. Because there were no significant changes over days for the repetition measure, and in order to obtain enough observations for an accurate estimation of behavior, the data for each animal were averaged over Days 1–6. Figure 5a shows the probability of a correct (i.e., nonrepetitive) choice as a function of serial choice position, that is, arm choices 1 to 6, corrected for chance. The probabilities were calculated as in Olton and Samuelson (1976, p. 106); chance performance was zero. As reported by Olton and Samuelson, mean probability of a correct choice decreased in successive choices, but remained above chance for all choices. Figure 5b shows the relative probability of a repetition as a function of the serial position of the original choice (corrected for opportunities), for the first five correct choices; this indicates a recency effect, whereby the probability of a repetition was highest for arms chosen early in the sequence, as found in eight-arm mazes (Olton and Samuelson). Figure 5c shows the relative frequency of all possible turn categories, measured up to criterion (all arms visited). The most frequent turn was two away from the previous choice.

Total activity (number of sensor activations) per session in the radial maze showed no significant changes either between or within groups over the 6 test days.

Discussion

The distribution of activity of rewarded rats in the Dashiell and radial mazes in this experiment could not be differentiated from that of nonrewarded rats, although speed of movement at the food locations was lower in the food-rewarded group in both mazes. In the Dashiell maze, food-rewarded animals did not learn to go straight from one food location to the next; area explored to criterion did not change significantly from the first to the last test day. Efficiency of exploration of the entire maze and the process of latent learning, as measured by the activity count to reach 36 different photocells, were unaffected by food reward.

In the radial maze, entries into the blind alleys decreased rapidly within the first few sessions in both groups. (This effect is not due to the animals' previous exposure to the Dashiell configuration, since we have consistently found the same pattern of avoidance behavior whether the animal has had previous exposure to other maze configurations or is maze naive; Isler, Oettinger, FitzGerald, & Bättig, in preparation). Food reward had no effects on arm choice behavior in terms of choice stereotypy or number of repetitions to criterion. As reported by others in elevated eight-arm mazes, a recency effect was apparent in the choice
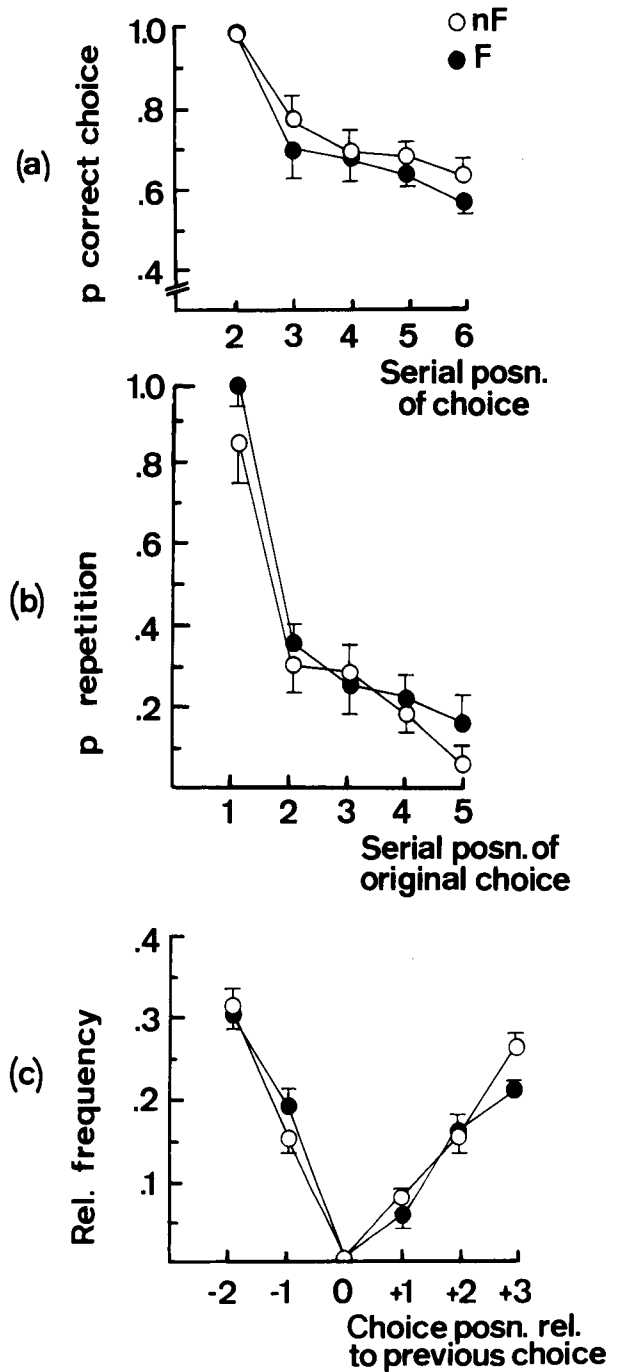

Figure 5. Arm choice behavior of the food-rewarded (F) and non-rewarded (nF) groups in the radial maze in Experiment 1 (animals at ad-lib body weights), pooled over the 6 test days. (a) Probability of a nonrepetitive arm choice as a function of the serial position of the choice; probability of a correct choice was above chance for all choices. (b) Probability of a repetitive arm choice as a function of the serial position of the original correct choice; probability of repetition was highest to arms chosen early in the sequence. (c) Relative frequencies of turn categories in the choice sequence to criterion (all arms visited); +2 was the most frequent turn category in both groups. The formulae for calculation of (a) and (b) were taken from Olton and Samuelson (1976). All values are expressed as means ± SEM.

behavior of all animals. The most preferred turn direction was two arms away from the previous choice; in eight-arm mazes, entering adjacent arms is apparently more likely (Yoerg & Kamil, 1982). Notably, patrolling efficiency in the radial maze was stable over days; there was no change in number of repetitions to criterion with repeated testing, and spontaneous patrolling was indistinguishable from food-rewarded patrolling in this respect.

Overall, the results indicate that rats will spontaneously patrol relatively complex mazes in a manner that is virtually indistinguishable from that of animals running for food reward. It is perhaps rather surprising that food reward had so little effect on the animals' behavior. By using animals at ad-lib body weights, we were concentrating on normal spontaneous behavior in this experiment. As a strong test of the effects of food reward, we tested animals deprived to 80% of ad-lib body weights in a second experiment.

EXPERIMENT 2

In this experiment we used basically the same procedure as in Experiment 1, but with animals deprived to 80% of ad-lib body weights to increase the incentive value of the food reward.

One aspect of behavior that we noticed in Experiment 1, but which we did not attempt to quantify, was that all animals continued to be active after visiting the food locations. In Experiment 2, we looked in detail at behavior occurring after criterion was reached, that is, with no food now present for the rewarded group.

Method

There were several differences in method with respect to Experiment 1. Three-month-old female, instead of male, RHA/Verh rats were used (no males were available). Ad-lib body weights at the beginning of the experiment were between 180 and 200 g. A total of 16 animals (8 per group) were used. Beginning 1 week prior to testing, feeding times were adjusted so that all animals' body weights were reduced by 20%, and were so maintained throughout the experiment. The apparatus was the same as described for Experiment 1, but movement of the animal through the maze was measured by underfloor electromagnetic field-effect sensors. In order

to obtain as much information as possible on behavior occurring after criterion had been reached, test duration was increased from 4.5 to 10 min, and the number of tests in each maze was increased from six to eight. This procedure was successful; most of the animals in both rewarded and nonrewarded groups reached criterion a second time, that is, revisited all food locations. We could therefore analyze the effects of food reward, not only by comparing the behavior of rewarded and nonrewarded animals up to criterion (first "round" of activity) as in Experiment 1, but also by analyzing changes in behavior in the food-rewarded group from the first to the second round, that is, with and without food reward. All other procedural details were as described in Experiment 1.

Results and Discussion

Dashiell maze. With one exception on Day 2, all animals in both rewarded and nonrewarded groups visited the six food locations on every test day, and most animals in both groups revisited all food locations within the 10 min trial (Table 2). Figure 6 shows behavior in terms of mean time, explored area, activity count, and activity distribution to criterion on each of the 8 days of the experiment. Behaviors during the first and second rounds of activity (i.e., all food locations visited, and all food locations revisited) are shown in the left and eight panels, respectively, of Figure 6. Those animals that failed to complete a second round were assigned the values reached at the end of the session. The single animal that failed to complete a first round on Day 2 was assigned, as scores for Round 2 on this day, means of its Round 2 behavior over the other 7 days.

During the first round of activity, the rewarded group was significantly faster to criterion, explored a smaller area, had lower activity, and was relatively more active in the outer parts of the maze than the nonrewarded group over all days [group $Fs(1,14) > 12$]. Despite the apparent increasing difference between the two groups from the start to the end of the experiment, seen in Figure 6, significant session and session × food reward effects occurred only for the activity distribution measure [$F(7,98)=2.6$], apparently because the food-rewarded group was relatively more active in the outer part of the maze on Days 3–8 than the nonrewarded animals. These results indicate that the food-rewarded animals in this ex-

Table 2
Number of Rats in Experiment 2 Reaching Criterion
(All Food Locations) for the First and Second Time on Each Test Day

Round	Dashiell								Radial							
	Day 1	Day 2	Day 3	Day 4	Day 5	Day 6	Day 7	Day 8	Day 1	Day 2	Day 3	Day 4	Day 5	Day 6	Day 7	Day 8
Food-Rewarded Group																
1	8	8	8	8	8	8		8	8	7	8	8	8	8	8	8	8
										(8)	(8)	(8)	(8)	(8)	(8)	(8)	(8)
2	8	8	8	7	8	8		8	7	4	5	7	8	8	7	7	6
										(6)	(7)	(8)	(8)	(8)	(8)	(8)	(6)
Nonrewarded Group																
1	8	7	8	8	8	8		8	8	7	8	7	8	7	8	7	7
										(8)	(8)	(8)	(8)	(8)	(8)	(8)	(8)
2	8	7	8	6	7	6		7	5	0	4	3	4	3	3	2	3
										(6)	(8)	(6)	(6)	(8)	(6)	(6)	(8)

Note—Numbers in brackets are the number of rats reaching criterion (middle of all arms) in the radial maze.
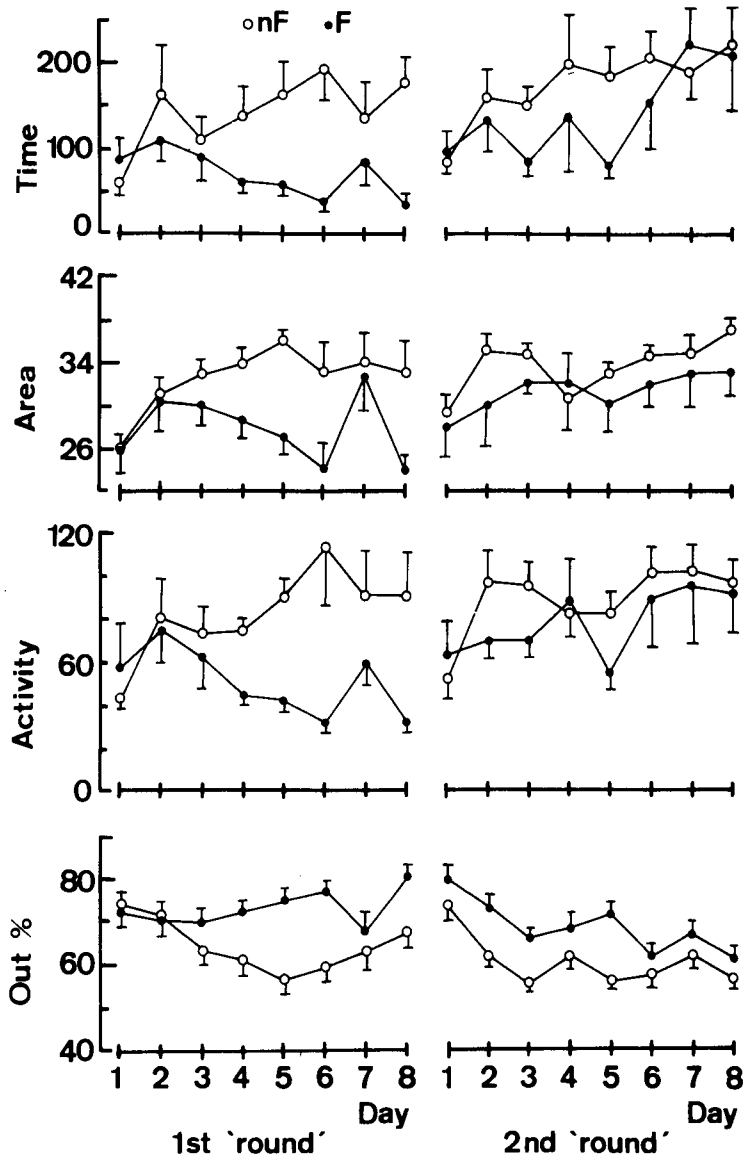
Figure 6. Behavior of food-rewarded (filled circles) and nonrewarded (open circles) groups to criterion (all food locations visited) in the Dashiell maze in Experiment 2 (animals at 80% of ad-lib body weights). The left panel shows behavior until criterion was reached for the first time; the right panel shows behavior until criterion was reached a second time, that is, until all food locations were revisited. From top to bottom: time in seconds to criterion; explored area, expressed as the number of different sensors activated; activity to criterion, measured by the number of sensor activations; and activity distribution, expressed as the percentage of activity occuring in the outer parts of the maze. All values are expressed as means ± SEM.

periment did move more directly from one food location to the next than the nonrewarded animals, until all food locations had been visited.

During the second round of activity, until all the food locations were revisited (with no food now present for either group), behavior of the two groups did not differ significantly in terms of time, area explored, or activity to criterion. Relative activity in the outer part of the maze, however, was significantly higher in the rewarded than in the nonrewarded group, as it had been during the first

round. Repeated measures comparison between Rounds 1 and 2 showed that there were no significant changes in behavior in the nonrewarded animals, but that the food-rewarded group took longer, explored a greater area, and had higher activity counts to revisit the (previous) food locations than when they were visiting them for the first time. Relative activity in the outer part of the maze did not change significantly in the rewarded group from Round 1 to Round 2. It is particularly interesting that the behavior of the rewarded animals was so similar to that

of the nonrewarded animals during the second round: Having consumed all the available food, they behaved much like animals that had never found food in the maze, except that they were relatively more active in the outer part of the maze, where they had previously fed.

Efficiency of patrolling the entire maze, independent of behavior to criterion, improved over sessions as in Experiment 1, as measured by the activity count to reach 36 different sensors [session $F(7,98)=4.8$]. There were

no main or interaction effects of food reward on this behavior. Total activity in the Dashiell maze decreased significantly over days during this experiment [$F(5,140)=6.4$], but was not affected by food reward.

Radial maze. At least 7 of the 8 animals in each group visited all arm ends (food locations) on every test day. During the second round, as shown in Table 2, more rewarded than nonrewarded animals revisited all arm ends—significantly more, by Fisher exact probability test,
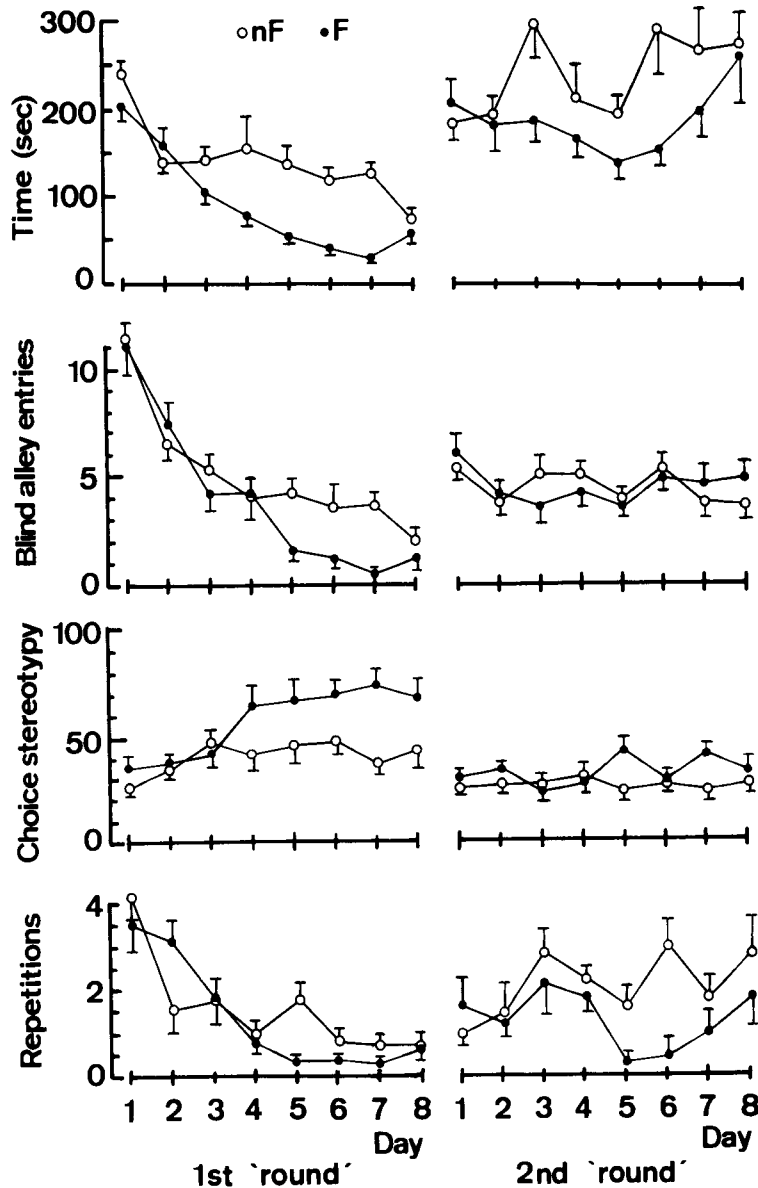

Figure 7. Behavior of food-rewarded (filled circles) and nonrewarded (open circles) groups to criterion (all arms visited) in the radial maze in Experiment 2 (animals at 80% of ad-lib body weights). The left panel shows behavior until criterion was reached for the first time; the right panel shows behavior until criterion was reached a second time, that is, until all arms were revisited. From top to bottom: time in seconds to criterion: number of blind alley entries; choice stereotypy, expressed as percent frequency of the most frequent turn category (see Method, Behavioral Measures section); and number of repetitive arm visits. All values are expressed as means ± SEM.

(Siegel, 1956) on Days 5 and 7. Nonetheless, as shown in brackets in Table 2, most of the nonrewarded animals did reenter all arms, reaching at least their midpoints.

Figure 7 shows the behavior of rewarded and nonrewarded groups during the first and second rounds of activity in terms of mean time, blind alley entries, choice stereotypy, and number of repetitions to criterion. During the first round of activity, until all arms were visited for the first time, the food-rewarded rats were significantly faster to criterion than the nonrewarded rats over all 8 days [F(1,14)=31.9]. [There was also a group × session interaction effect for this time measure, F(7,98)=2.2, probably because the rewarded group ran increasingly faster on Days 3-6, whereas the nonrewarded group did not.] The only other significant effect of food reward was on choice stereotypy, which was significantly higher overall in the food-rewarded group [F(1,14)=7.4]. As in Experiment 1, the number of blind alley entries to criterion decreased in all animals over days [F(7,98)=32.9], and was not significantly affected by food reward. In contrast to Experiment 1, the number of repetitive arm entries to criterion decreased over days [F(7,98)=8.3]; both rewarded and nonrewarded groups made significantly fewer repetitions to criterion on Day 8 than on Day 1 (by related t test). From these results it can be concluded that, as in Experiment 1, food reward did not affect behavior in terms of blind alley entries and repetitive arm entries to criterion. The increase in choice stereotypy in the rewarded group may have arisen because this group was running faster than the nonrewarded group. Olton, Collison, and Werz (1977) reported a similar increase in choice stereotypy with repeated testing in the elevated radial maze with food reward; stereotypy was reduced by delaying the animal between choices.

We also analyzed radial maze behavior in terms of commonly reported measures of choice performance. The results are shown in Figure 8. As in Experiment 1, the mean probability of a correct choice decreased in successive choices, but remained above chance for all choices; a recency effect was also apparent, whereby the probability of a repetition was highest for arms chosen early in the sequence. Neither of these measures was affected by food reward. Turn behavior did appear to differ between the two groups: for the nonrewarded animals, the most frequent turn was two away from the previous choice, whereas in the food-rewarded animals, it was one away from the previous choice. This difference, however, was not significant by repeated measures (group × turn category) ANOVA. It is interesting in this context to note that the most preferred turn direction of food-deprived rats in eight-arm maze experiments is often also into adjacent arms (Yoerg & Kamil, 1982). Both this effect and the increased choice stereotypy in these rewarded animals may be attributable to their trying to get around the maze as quickly and with as little motor effort as possible. However, it is also possible that the rats were attempting to reduce memory load (i.e., were using adjacent turn-
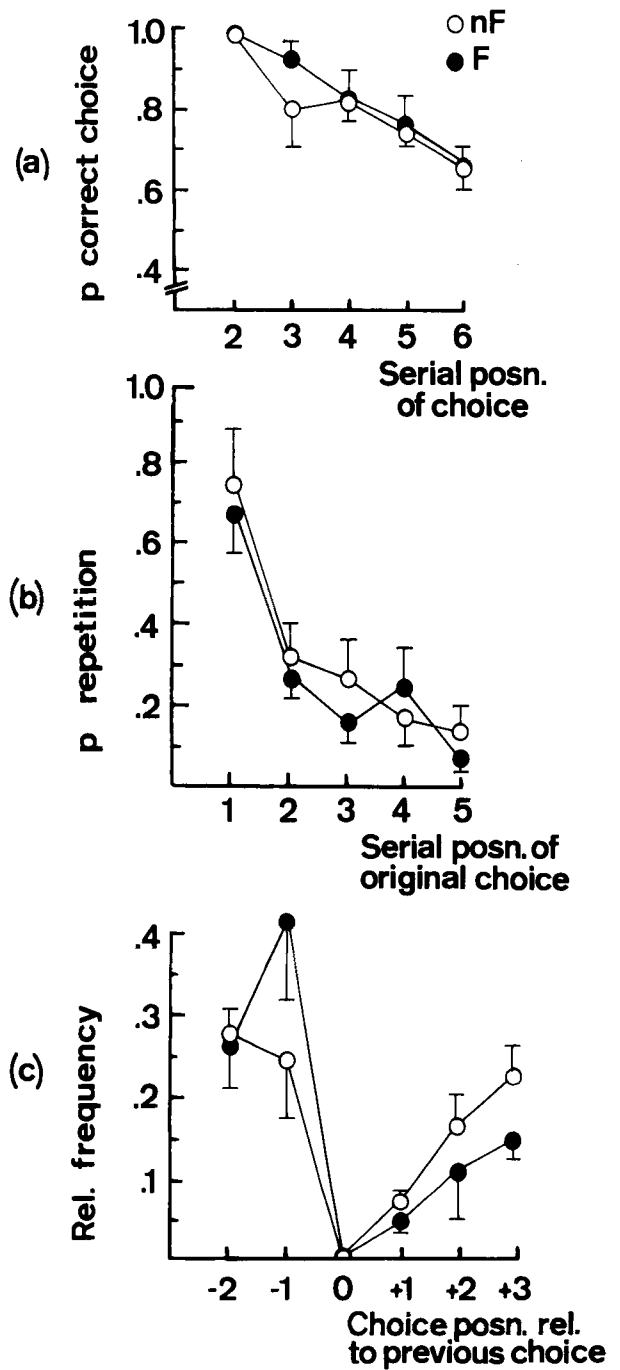

Figure 8. Arm choice behavior of the food-rewarded (F) and nonrewarded (nF) groups in the radial maze in Experiment 2 (animals at 80% of ad-lib body weights), pooled over the 8 test days. (a) Probability of a repetitive arm choice as a function of the serial position of the choice; probability of a correct choice was above chance for all choices. (b) Probability of a repetitive arm choice as a function of the serial position of the original correct choice; probability of repetition was highest to arms chosen early in the sequence. (c) Relative frequencies of turn categories in the choice sequence to criterion (all arms visited); 11 (adjacent arm) was the most frequent turn category in the food-rewarded group. The formulae for calculation of (a) and (b) were taken from Olton and Samuelson (1976). Points represent mean values ± SEM.

ing as a response algorithm). To test this possibility, it would be necessary to artificially interrupt the animals' choice behavior in some way.

During the second round of activity, more animals in the rewarded group than in the nonrewarded group revisited all of the arm ends (Table 2). However, most of the animals in both groups reentered all arms a second time (Table 2, numbers in brackets). The right-hand panel of Figure 7 shows behavior during this second round, until all arms were reentered.

Over the 8 test days, the rewarded animals were significantly faster to criterion in Round 2 than the nonrewarded animals [F(1,14)=4.6]. The two groups did not differ in number of blind alley entries and choice stereotypy, but the rewarded animals made fewer repetitions to criterion than the nonrewarded group in this second round [F(1,14)=8.9].

Comparison of behavior between the first and second rounds showed that both groups were slower to criterion in the second round than in the first [Fs(1,7) > 22]. There was no significant overall change in number of blind alley entries in either group from Round 1 to Round 2, but there were significant session × round interaction effects in both groups [Fs(7,49) > 4], apparently because, for both groups, blind alley entries decreased over the 8 days of testing in the first round but remained constant during the second round. Over all 8 days, choice stereotypy was significantly lower during the second round than during the first in both groups [Fs(1,7) > 35]. In both groups, the mean number of repetitions during Round 2 was lower than that during Round 1 on Days 1 and 2, but on Days 3-8, both groups made more repetitions in the second than in the first round. This was reflected in a significant session × round interaction for both groups [F(7,49) > 2.4], without significant main group effects.

The results for this second round of activity indicate that the previous experience of food reward did influence subsequent nonrewarded maze activity. First, more rewarded than nonrewarded animals revisited all the arm ends. Second, although the rewarded animals were slower to visit all arms in the second than in the first round, they were still faster in Round 2 than the nonrewarded animals. Third, nonrewarded animals made more repetitive visits to criterion in the second round than the rewarded animals. This effect in the nonrewarded animals may not be reliable: we have run replications of the experiment in which nonrewarded animals patrolled as efficiently as rewarded animals during the second round.

The parallel changes in choice stereotypy and time to criterion from first to second round in both groups (time to criterion increased and choice stereotypy decreased) lends support to the idea that choice stereotypy is at least partly determined by running speed (see Magni, Krekule, & Bures, 1979; Olton, Collison, & Werz, 1977). There was apparently no simple relationship between choice stereotypy and patrolling efficiency, in terms of repetitive arm entries, since choice stereotypy was higher overall in the rewarded than in the nonrewarded group in

Round 1, but the number of repetitions made by the two groups was not significantly different. This finding is in agreement with the findings of Magni et al. (1979), Olton et al. (1977), and Yoerg and Kamil (1982).

Total activity per session, independent of criterion, changed significantly over days [F(7,98)=11.8], but was not affected by food reward; it increased significantly in both groups from Day 1 to Day 8.

Overall, the results of this experiment indicate that hungry rats will minimize the time required to visit food sources. When given the opportunity (i.e., in the Dashiell maze), they move more directly between food sources, but when the path available for exploration is the same as that required to reach the food sources, their efficiency of patrolling is the same as that of spontaneously exploring animals.

GENERAL DISCUSSION

The first purpose of this study was to describe the spontaneous patrolling behavior of rats in the radial tunnel maze and compare it with that of food-rewarded rats. The results indicate that patrolling behavior in terms of avoidance of already-visited arms was virtually unaffected by food reward, whether the animals were at ad-lib body weights or were food-deprived to 80% of ad-lib weights. In both experiments, furthermore, patrolling behavior was comparable to that reported by Olton and Samuelson (1976) for rewarded animals in the elevated eight-arm maze. Several aspects of patrolling behavior did, however, differ between the first and second experiments. In Experiment 1, there was no change in patrolling efficiency over days, whereas in Experiment 2 all animals became more efficient with repeated testing. Also, over all sessions, the animals in Experiment 2 patrolled more efficiently than those in Experiment 1. Turn choice behavior also differed: the most frequent turn direction in Experiment 1 was two away from the previous choice for both rewarded and nonrewarded groups, whereas in Experiment 2, the rewarded group tended to enter adjacent arms more frequently. Further experiments will be necessary to determine whether these differences between Experiments 1 and 2 are attributable to the higher level of deprivation of the subjects in Experiment 2. Also, we cannot rule out the possibility that sex is an important factor: male rats were used in Experiment 1, females in Experiment 2. Despite the differences in arm choice behavior between the two experiments, it can be concluded from these results that nonrewarded rats will spontaneously patrol the radial maze as efficiently as rats that are rewarded for doing so.

The second aim of the study was to seek evidence for win-shift and win-stay behavior produced by food reward. Win-shift effects of food reward should have been observable in the Dashiell maze as a reduction in relative activity at the food locations. In Experiment 1, activity distribution was unaffected by food reward. In Experiment 2, relative activity was actually higher at the food locations

in the rewarded than in the nonrewarded rats over all sessions: this behavior is the opposite of that which would be expected if food reward increases the probability of shifting. Since win-shift effects may have disappeared with repeated testing as the animals learned where the food sources were located, we also looked in detail at behavior on the first test day. However, there was no significant change (by related t test) in activity distribution from Round 1 to Round 2 in either group on this day (nor was there any Round 1-Round 2 change for any other behavioral measure on Day 1). On the basis of these results, we conclude that there is no evidence for win-shift behavior by rats in the Dashiell maze; that is, there is no evidence that the probability of moving to less familiar or less frequently visited locations is increased by food reward. In the radial maze, providing food reward did not affect the number of repetitions; that is, animals that did not find food in the maze shifted as efficiently as animals that did find food.

A systematic confound in the design of the present study was that all animals were tested in the radial maze after previous experience in the Dashiell configuration. This means that when tested in the radial maze for the first time, they were already familiar with the maze apparatus, and had an expectancy of reward or no reward. This expectancy might be expected to produce an increase in shift by the rewarded animals during the first radial maze test, because, in the immediately preceding Dashiell maze tests, they had encountered food pellets which were not replaced after consumption (i.e., a depletion condition, see Haig et al., 1983). The data from the first test day in the radial maze are crucial in this respect: analysis by t test revealed no significant differences in any behavioral variable between the rewarded and nonrewarded groups on the first radial maze test in Experiment 2. In Experiment 1, however, the rewarded animals made significantly more repetitions to visit all arms on the first radial maze test day than the nonrewarded animals, suggesting that food reward, rather than increasing shift behavior, actually increased stay behavior. We have subsequently run experiments comparing food-rewarded and nonrewarded radial maze behavior in test-naive animals (Isler et al., in preparation); the results suggest that naive animals do not behave in exactly the same way as animals with previous maze experience, but the overall conclusions concerning the effects of food reward on patrolling are the same.

We use the term "win-stay" to refer to the win-stay associative principle given in Gaffan and Davies (1982): that naive animals tend to expect food (or no food) in circumstances or places in which they have previously experienced it, and subsequently prefer stimuli associated with food to those associated with none. We found evidence for win-stay behavior in both Dashiell and radial mazes in Experiment 2. In the Dashiell maze, although there were no differences in behavior between rewarded and nonrewarded rats on the first test day, the rewarded rats were subsequently (over all 8 test days) relatively more active in the vicinity of the food locations than the nonrewarded rats during Round 1, until all the food had

been consumed. Even after all the food had been eaten (i.e., during Round 2), the rewarded animals, although they explored as much of the maze as the nonrewarded animals, were still relatively more active in the vicinity of the food locations. In the radial maze, there was no evidence for win-stay behavior during the first round, until all food locations had been visited for the first time: the number of arm repetitions and blind alley entries did not differ significantly between rewarded and nonrewarded groups. During the second round, however, more rewarded than nonrewarded animals returned to all six food locations at the ends of the arms (Table 2). Nonetheless, patrolling efficiency of the rewarded animals did not differ over all eight sessions between the first (rewarded) and the second (nonrewarded) round. In order to assess the immediate effects of finding food reward in the radial maze, we also examined changes in behavior from Round 1 to Round 2 on the first test day. Both rewarded and nonrewarded groups made fewer blind alley entries in the second than in the first round (by related t test). The nonrewarded animals were quicker in the second round than in the first and made significantly fewer repetitions, but the rewarded animals' speed and efficiency of patrolling did not change significantly from the first to the second round on this first radial maze test. This could be taken as evidence for win-stay behavior by the rewarded rats.

Given that the differences between rewarded and nonrewarded animals are explicable in terms of win-stay associative learning, the overall similarity of their behavior implies that the major determinant of patrolling in these mazes, whether or not food reward is provided, is a spontaneous tendency to avoid places recently visited (see Gaffan & Davies, 1981; Haig et al., 1983).

Two aspects of the spontaneous maze patrolling behavior described here deserve particular emphasis. First, it appears to be genuinely spontaneous: all animals, both rewarded and nonrewarded, patrolled both mazes on first exposure to them. Rats running for food reward on elevated radial mazes, by contrast, typically require 1 to 2 weeks' shaping and training before they will run reliably and efficiently (e.g., Olton & Samuelson, 1976; but see Bruto & Anisman, 1983, for a description of spontaneous elevated radial maze patrolling by mice). The second point is that activity levels remain high in nonrewarded animals, even after many days of testing in the same apparatus (up to 30 consecutive days; Isler, Oettinger, FitzGerald, & Bättig, unpublished observations). Such behavior does not occur in open-field tests, in which activity usually declines with repeated exposure, or in elevated mazes, in which the animal will cease to run if reward is withheld. Perhaps the resemblance of this tunnel maze apparatus to the rat's natural burrow habitat (Lore & Flannelly, 1978) is important; certainly, the situation appears to be relatively nonstressful to the rat (defecation and urination during testing are extremely rare).

The application of optimal foraging theory to rat behavior in the laboratory is extremely fruitful (see, e.g., Fantino & Abarca, 1985; Kamil & Sargent, 1981). Un-

fortunately, the spontaneous behavior described here is apparently not easily amenable to such analyses. The problem is that optimal foraging deals with discrete instrumental events (i.e., the collecting of food) that can be measured and manipulated quite explicitly, whereas the rats spontaneously running around in these tunnel mazes are apparently collecting information of some kind. Furthermore, in the case of the nonrewarded animals in this study, the information they are collecting is from an unchanging, familiar environment. O'Keefe and Nadel (1978) assigned a primary role to mismatch as a causal factor underlying exploration, but acknowledged that familiar stimuli are also explored. They described such exploration as the animal's "mak[ing] a cursory check to ensure that nothing has changed" (p. 255). Exactly how one goes about quantifying and manipulating this information is as much of a problem today as it was 25 years ago, although further experimental progress should be possible, based on the significant developments in both learning and cognitive map theories that have been made since then (review in Toates, 1983). We are left with the suspicion that the optimal foraging behavior demonstrated by rats in mazes may be a special case of a more general phenomenon, optimal information foraging, whose investigation has been rather neglected.

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