Spatial Memory and Radial Arm Maze Performance of Rats

DAVID S. OLTON, CHRISTINE COLLISON, AND MARY ANN WEBZ
The Johns Hopkins University

Rats were tested on an elevated radial maze for their ability to choose each of 17 different arms once without repeating any choices. The first experiment indicated that the animals performed well, choosing an average of more than 14 different arms in the first 17 choices. Subsequent experiments demonstrated that: (a) response patterns, general algorithms, or intramaze markings were not necessary for correct choices; (b) there was interference among choices within a trial so that the probability of a correct response decreased as the number of choices increased; (c) there was no serial-order effect (primacy or recency); (d) animals tested in a procedure which did not require prior shaping showed no evidence of a general preconditioning effect on repeated choices. The results are discussed in terms of spatial memory.

Spatial stimuli exert a strong influence on animal discrimination behavior. Early maze experiments demonstrated that spatial mazes were learned rapidly and performed well (Vincent, 1915; Watson, 1907) without reliance on intramaze cues (Vincent, 1916; Watson, 1907) or patterns of responses (Drew and Gray, 1932; Laubach and McCarthy, 1936; MacFarlane, 1940). Later experiments investigating "reasoning" (Miller, 1959) or "inference" (Honzik & Telman, 1936; Tolman, 1933) in spatial tasks provided evidence that spatially organized behavior was remarkably flexible and could be altered rapidly, on the basis of minimal experience, to meet the demands of a changing environment. More recent quantitative analysis of stimulus control in spontaneous alternation (Douglas, 1960), active avoidance (Olton, 1973; Olton and Isaacson, 1968), and a variety of other tasks (see Sutherland & Mackintosh, 1971; particularly, Chapters 4, 5, and 13) support these conclusions, consistently demonstrating that spatial stimuli have a marked, perhaps unique, priority among intersensory stimuli in directing choice behavior.

On the assumption that this preference for spatial cues might reflect an enhanced ability to process information about spatial location, Olton and

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L. T. THOMPSON III

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Samuelson (1976) introduced a new spatial paradigm designed to investigate the characteristics of working memory. The apparatus was a radial eight-arm maze, with the eight arms radiating away from the central platform like spokes on a wheel. At the beginning of each test, one pellet of food was placed at the end of each arm. Food-deprived rats were placed on the center platform and were allowed to choose freely among the arms until all eight pieces of food were obtained. The optimal strategy with this reward contingency is to choose each arm once and not repeat choices to any arm. The rats performed well, choosing an average of more than 7.5 different arms within the first eight choices. They did not rely on response chains, general algorithms, or intramaze marks to choose correctly. Olton and Samuelson (1976) argued that the animals formed in working memory a list of places which had been chosen and which should not be repeated. This list was developed as animals made their choices, so that, after each correct choice, another item (i.e., place) was added to the contents of the working memory. (For a formal model, see Olton 1977.) Working memory was described as having the following characteristics: (i) capacity to process accurately at least eight different items; (ii) interference among items so that, as the number of places chosen (and the number of items in working memory) increased, the probability of a correct response decreased; (iii) perfect retention (i.e., no decay) for periods up to 1 min. (iv) a slight recency effect as indicated by a decreased probability of making an error by immediately repeating previous correct choices (i.e., choices near the end of the list of places in memory); (v) no primacy effect as indicated by no decrease in the probability of making an error by repeating the first few correct choices of each test (i.e., choices near the beginning of the list of places in memory).

Although Olton and Samuelson (1976) were able to provide considerable information about the characteristics of working memory, the conclusions of their experiments were limited by several factors. First, the task was easy, and the animals often performed perfectly, making an accurate estimate of the capacity of working memory almost impossible and providing only limited information for the data analyses based on errors. Second, all animals received considerable shaping experience prior to actual testing and performed well even on the first few days, so that the relative roles of learning and species-specific response predispositions could not be assessed (see Seligman & Hager, 1972). Third, no attempt was made to determine the effects of eliminating preferred response patterns upon spatial memory.

The present series of experiments was designed to address each of the issues mentioned above. First, a radial arm maze with 17 arms was used to provide a more difficult test (Expts 1 and 2). Second, some animals with no prior shaping were tested to assess the role of learning (Expt 3). Third, a new procedure was developed that effectively disrupted the response patterns seen in the standard paradigm (Expt 4). The rationale for each experiment is further described in the introduction to that experiment.

**EXPERIMENT 1**

Rats performed so well in the eight-arm apparatus that analyses based on errors had few data, and no estimate of the limits of the capacity of working memory was possible. To alleviate these difficulties, a 17-arm apparatus was constructed. By more than doubling the number of alternatives presented on each choice, this apparatus made the task more difficult, providing more errors for analysis and enabling a better estimate of the amount of information that can be processed accurately in working memory.

**Method.** The subjects were 17 male albino rats, approximately 90 days old at the start of testing. They were housed in standard individual rodent cages with ad lib water. Food was provided approximately 1 hr after daily testing. Food was provided approximately 1 hr after the last 3 g of deprivation body weight, with an additional 3 g to the next animal. To partially compensate for the body growth that would be expected to take place.

**Apparatus.** The apparatus was a wooden 17-arm radial maze elevated 65 cm above the floor. The center platform was 87 cm in diameter. Each arm was 69 cm long and 10 cm wide. A partition 32 cm long and 12 cm high was attached to one side of each arm, at the end nearest to the center platform, to prevent the animals from stepping directly from one arm to another without entering the center platform. A 3-cm-high guard was attached to both sides of the remainder of each arm. A hole 2 cm in diameter and 1 cm deep at the outer end of each arm served as a food cup. The arms were placed equidistant around the center platform so that the angle between them was 21°. The room containing the apparatus was large and well illuminated with a variety of objects in it.

**Procedure.** Animals were shaped to run on the apparatus by first placing food at the entrance to the arms near the center platform and then placing food farther out on the arms until the animals ran to the end of the arms without hesitation. For 11 animals, shaping took place in a fixed manner over 6 days. For the remaining six animals, shaping took place at a variable rate, depending on the animals' performance, and required from 3 to 15 days.

Each animal was given one test daily, 5 days per week for the next 6 weeks. One 190-mg Noyes food pellet was placed at the end of each of the 17 arms. The animal was placed on the center platform of the apparatus and was allowed to choose freely among the arms until all 17 pieces of food had been obtained or until a total of 15 min had passed. At the end of each trial,
each animal was returned to its home cage and, after approximately 1 hr, was given sufficient food to maintain body weight at the appropriate level.

Statistical analysis. All differences reported as statistically significant were evaluated by either a $t$ test or a one-way analysis of variance and resulted in a $p$ level less than .01, two-tailed.

Results

On the first few days of shaping, animals spent most of their time on the center platform or on the arms next to the partitions and went to the ends of the arms only after considerable hesitation. By the end of shaping, however, all animals ran to the ends of the arms without difficulty. During testing, each animal would typically approach the entrance to an arm and orient toward the end of it. On the first few choices of each day, an arm was usually entered without delay. Near the end of each day's test, animals would often approach an arm, orient toward the end of it, and, while still standing on the center platform, pause, often for several seconds, before either entering the arm or approaching a different arm. Once all four feet had been placed on an arm, animals almost inevitably went directly to the end of the arm without hesitation before turning around and returning to the center platform. When leaving an arm and entering the center platform, each rat tended to turn consistently in either a clockwise or counterclockwise direction on any particular day and usually skipped at least one but not more than four arms before making the next choice.

The animals performed well, and the mean number of different arms chosen in the first 17 choices of each day for Days 1–10, 11–20, and 21–30 was 14.0, 14.6, and 14.5, respectively. Since the chance probability of choosing 14 or more different arms within the first 17 choices on any single day is .02 (see Feller, 1950, pp. 69–70), performance was clearly far above that expected on the basis of random choices. In general, choice accuracy was greatest at the beginning of each day’s test and declined gradually as the number of choices increased. Figure 1 presents these data as a transformed probability of a correct response for choices 2–17. The transformation takes into account the changing chance probability of a correct response and expresses the result as a percentage maximum performance score. Scores can range from 1.0, indicating a correct response at every opportunity, through 0.0, indicating random performance, to −1.0, indicating an incorrect response at every opportunity. The formulae used for obtaining these scores were:

\[
\text{if } p(\text{cor})_{\text{obs}} > p(\text{cor})_{\text{exp}}, \quad \frac{p(\text{cor})_{\text{obs}} - p(\text{cor})_{\text{exp}}}{1 - p(\text{cor})_{\text{exp}}} \tag{1a}
\]

\[
\text{if } p(\text{cor})_{\text{exp}} > p(\text{cor})_{\text{obs}}, \quad \frac{p(\text{cor})_{\text{obs}} - p(\text{cor})_{\text{exp}}}{p(\text{cor})_{\text{exp}} - 0} \tag{1b}
\]

where $p(\text{cor})_{\text{obs}} = (\text{number of correct responses})/(\text{total number of responses})$ and $p(\text{cor})_{\text{exp}} = (\text{number of arms not yet chosen})/17$ (for further explanation, see Olton & Samuelson, 1976). Data are not presented for the first choice of each day because this choice had to be correct, nor are they presented for choices greater than 17 because the animals occasionally performed perfectly so that no data were available for these choices. As can be seen from the figure, choice accuracy was almost perfect at the beginning of each day’s test, but gradually declined as the number of choices increased. An important point is that, even on the seventeenth choice, the mean score for every animal for every block of 10 days was greater than chance, indicating that the animals were still performing correctly on the seventeenth choice. There was a slight but significant increase in accuracy for each choice from Days 1–10 to 11–20 reflecting the slight increase in the number of different arms chosen within the first 17 choices reported earlier.

When errors occurred, they were less likely to be made by repeating the last few correct choices of each test, as indicated by the relative probability of repeating a choice per opportunity. In this analysis, scores can range from 0, indicating that no errors were made by repeating the choice in question, to some positive number. The greater the score, the greater the relative probability of an error being made to the choice in question. These scores were obtained from the relative probability of making an error by repeating each of the previous correct choices divided by the number of
opportunities to repeat each previously correct choice according to the formula:

\[ p(\text{rep})_{\text{obs}} / N_{\text{oppa}} \times 100, \]

where \( p(\text{rep})_{\text{obs}} \) = (number of repetitions of previously correct choice)/(total number of repetitions) and \( N_{\text{oppa}} \) = number of choices (opportunities) after correct choice. (Further explanation is provided in Olton & Samuelson, 1976.) As can be seen from Fig. 2, the relative probability of making an error by repeating a particular correct choice was relatively low for the last few choices.

For readers who wish to conduct additional analyses, the Appendix presents the daily results from six rats, Days 21-30, choices 1 through 27. For each animal, the number of each choice indicates the arm which was chosen. Arms were numbered sequentially clockwise.

**Discussion**

Results from the current 17-arm radial maze generally support two of the conclusions drawn previously from an eight-arm radial maze (Olton & Samuelson, 1976). First, animals performed well, choosing many more correct arms than expected by chance, even on the seventeenth choice of the test. Second, choice accuracy decreased as the number of choices increased, suggesting interference among the memories of each choice. The results question two other conclusions. First, although specific response chains were not used by the animals in the present paradigm, there were two strong response tendencies: (a) turning in either a clockwise or counterclockwise fashion and (b) skipping between one and four arms before making the next choice. Although choice behavior in the eight-arm maze did not meet the criteria for true randomness (Bryant & Church, 1974; Church, personal communication), it was much less patterned than observed here. Second, the probability of making an error by repeating correct choices just prior to the choice in question decreased only slightly from choices 2 to 17, with most of the decrease taking place only on the last few choices of the test. This decrease was referred to as a “recency effect” by Olton and Samuelson, because it indicates that, when errors occurred, they were least likely to result from repetition of choices just previously made, i.e., choices that were at the end of the list of places in working memory. In light of the response tendencies described above, most of the recency effect, and certainly that on the last few choices, might have been due to these response patterns. In these two respects, then, the results of the present experiment appear to be at variance with the results of the previous experiments and raise the question as to what extent the accuracy of choice behavior and the evidence of a recency effect reported here are artifacts of response processes rather than indications of mnemonic ones.

Each of the next three experiments was designed to address a specific question about the performance of animals in Expt. 1. Experiments 2, 3, and 4 evaluate, respectively, the influences of a possible intramaze marking system, the shaping procedure, and the response tendencies described above.

**EXPERIMENT 2**

The first experiment demonstrated that animals performed well on the 17 arm radial maze, choosing an average of more than 14 different arms within the first 17 choices. Olton and Samuelson (1976) demonstrated that rats solved the eight-arm radial maze test by identifying each of the different spatial locations and remembering which ones had been chosen. However, there are several ways of markedly simplifying the task and reducing the information that must be stored in memory in order to perform accurately. One such strategy would be to use an intramaze marking system so that the rodent equivalent of a check mark would be left on each arm as it was chosen. If such were the case, the animal would need only approach an arm, determine whether or not it contained a mark, and choose appropriately, rather than maintaining information about each of the chosen arms in working memory. Several studies have suggested that rats might leave “odor trails” which serve as discriminative stimuli...
Douglas, 1966; Wasserman & Jensen, 1969). The likelihood that an "odor trail" or any other intramaze marking system could accurately direct choice behavior in the present paradigm is very remote (see discussion in Means, Hardy, Gabriel, & Uphold, 1971; Olton & Samuelson, 1976; Olton, 1977). Nonetheless, use of an intramaze marking system is a logical approach to solving the radial arm maze paradigm and must be examined. In the present experiment, spatial location and intramaze cues were treated as redundant relevant cues. On control days, these cues remained redundant. On test days, these two sets of cues were separated so that they were no longer redundant, and an evaluation was made of the relative amount of control exerted by each cue on choice accuracy.

Method

Subjects and apparatus. The subjects and apparatus were the same as in Expt 1.

Procedure. Since the testing procedure required that animals be removed from the apparatus while arms were being interchanged, the animals were first given 5 days of testing to accustom them to this procedure. Each day, the animal was allowed to make five choices, was removed from the apparatus, was placed in the home cage on the floor at the side of the room, and then was returned to the apparatus several minutes later. During the time the animal was in the home cage, no alterations were made to the maze. Following shaping, the testing procedure outlined below was instituted.

Control. Animals were placed on the apparatus as usual and were allowed to choose five different arms. They were then removed from the apparatus and returned to their home cage for approximately 2 min. During this time, the experimenter moved the arms chosen by the animal back and forth but left them in their original positions; the position of food reward was unchanged. Thus, the procedure was the same as in Expt 1, except that animals were removed from the apparatus between the fifth and sixth choices.

For the two experimental conditions to be described below, arms were interchanged after the fifth choice while the animal was in his home cage. The following terminology will be used to identify the arms and spatial locations at the time the animal was removed from the apparatus after the first five choices. "Chosen arm" will refer to an arm chosen prior to removal, "chosen spatial location" will refer to the spatial location of an arm chosen prior to removal, "unchosen arm" will refer to an arm not chosen prior to removal, and "unchosen spatial location" will refer to the spatial location of an arm not chosen prior to removal.

Switch arms 1–5, rehabilitate all arms procedure. For the "Switch arms 1–5, rehabilitate all arm" (S1-5RA) procedure, animals were placed on the apparatus as usual, were allowed to choose five different arms, and then were removed to their home cages. The five chosen arms were then interchanged with the nearest five unchosen arms, and food pellets were replaced at the end of the five chosen arms which did not have food, so that all arms contained food. The animal was returned to the center platform of the apparatus and was allowed to choose freely until a total of 17 food pellets (i.e., 12 food pellets after replacement on the apparatus) had been obtained.

Switch arms 1–5, rehabilitate spatial locations procedure. The "Switch arms 1–5, rehabilitate spatial locations" (S1-5RS) procedure was identical to S1-5RA in that animals were allowed to choose any five arms and were removed from the apparatus, and the five chosen arms were interchanged with the nearest five unchosen arms. Here, the procedure differed from S1-5RA, because food pellets were removed from the five unchosen arms and were placed on the five chosen arms. As will be described in the Results section, there was a slight decrease in the number of different spatial locations chosen in the S1-5RA procedure as compared to the control condition. To the extent that the decrement in S1-5RA was due to a change in cues associated with the food location at the ends of the arms, performance in S1-5RS ought to be similar to performance in the control condition and better than that in S1-5RA. To the extent that the decrement in S1-5RA was due to nonfood related cues, performance in S1-5RS ought to be similar to that in S1-5RA and worse than that in the control condition.

Data Analysis

When the animal was returned to the apparatus after the arms had been interchanged in the S1-5RS and S1-5RA conditions, the five unchosen arms were in the five chosen spatial locations. If animals use an intramaze marking system to choose an arm, they ought to respond to the five unchosen arms, thereby repeating five chosen spatial locations, and ought not to respond to the five chosen arms, thereby reducing the total number of different spatial locations chosen after replacement on the apparatus. If animals do not use an intramaze marking system, they should be unaffected by interchanging arms, so that the number of repetitions of chosen spatial locations should not increase, and the total number of different spatial locations chosen in the first 17 choices should not decrease.

Two different formulae were used to obtain a quantitative estimate of the effects of interchanging arms on choice behavior. The first is sensitive only to repetitions of chosen spatial locations; the second is sensitive to all repetitions of spatial locations, both chosen and unchosen. For both formulae, to the extent that animals use intramaze arm cues, scores will be greater than .50 and will approach 1.00. To the extent that they ignore intramaze arm cues, scores will be less than .50 and will approach 0.

"$\text{Number of repetitions of chosen spatial locations after interchanging arms}$"
arms. To the extent that animals choose on the basis of intramaze arm cues, after the arms are interchanged, they ought to repeat chosen spatial locations in order to respond to unchosen arms, and the number of repetitions of chosen spatial locations ought to increase above the level found in control conditions. A quantitative measure of this tendency is obtained from the formula:

\[
(R_1 - R_e)/(N - R_e)
\]

(3)

where \( N \) = number of unchosen arms placed in chosen spatial locations; \( R_e \) = number of repetitions of first five spatial locations chosen on control days (i.e., errors); and \( R_1 \) = number of repetitions of first five spatial locations chosen on test days. If the animals use an intramaze marking system exclusively, they should repeat all unchosen arms which are in chosen spatial locations: \( R_1 = N \) and the result of the formula is 1.00. If the animals do not use an intramaze marking system at all, they should make no more repetitions of chosen spatial locations containing unchosen arms on test days than they make errors on control days: \( R_1 = R_e \) and the result of the formula is 0.

Number of different spatial locations chosen in the first 17 choices. Interchanging arms might influence responses to arms that were not interchanged as well as responses to arms that were interchanged. Such a result would indicate that the arm interchanging tended to confuse and disorient the animals in general, suggesting that they used some combination of intramaze cues and other cues in their choice behavior. A quantitative measure of choice accuracy to all arms is obtained from the formula:

\[
(S_e - S_1)/(N - R_e)
\]

(4)

where \( N \) = number of unchosen arms placed in chosen spatial locations; \( R_e \) = number of repetitions of first five spatial locations chosen on control days (i.e., errors); \( S_e \) = number of different spatial locations chosen within the first 17 choices on control days; \( S_1 \) = number of different spatial locations chosen within the first 17 choices on test days.

If the animals use an intramaze marking system exclusively, the number of spatial locations chosen within the first 17 choices on test days ought to decrease by \( N - R_e \), as compared to the value on control days, \( S_e - S_1 = N - R_e \), and the result of the formula is 1.00. If the animals use a complex conjunction of cues and all choice behavior is disrupted by interchanging arms, \( S_e - S_1 \) might be greater than \( N - R_e \), and the result of the formula would be greater than 1.00. If the animals do not use an intramaze marking system by itself or in conjunction with other cues, interchanging arms should make no difference in the accuracy of choice behavior; the number of different spatial locations chosen within the first 17 choices on test days should be the same as on control days, \( S_e = S_1 \), and the result of the formula is 0.

Results

During S1-5RA and S1-5RS, the number of different spatial locations chosen within the first 17 choices decreased slightly from control conditions, and the number of repetitions of the first five arms increased slightly. In all cases, however, the formulae giving a quantitative estimate of the importance of arm and food cues together (S1-5RA) and the importance of arm cues alone (S1-5RS) indicate that all animals used intramaze cues to a greater extent than they used extramaze cues (all scores were less than .50), and that the importance of intramaze cues was minimal (scores ranged from .69 to .17). These data are presented in Fig. 3.

Discussion

The minimal decrease in the accuracy of performance during test days, when chosen and unchosen arms were interchanged, as compared to
control days indicates that the rats made little if any use of an intramaze marking system to direct their choices. The similarity of performance in S1-5RS and S1-5RA indicates that the presence or absence of food at the end of an arm did not influence the animals' choices.

**EXPERIMENT 3**

The relative difficulty of the task in the 17-arm apparatus, as compared to the 8-arm apparatus, makes possible an assessment of the role of learning in performance of this task, a factor that has not been considered previously. Many experiments have demonstrated an important influence of "preparedness" (see Seligman & Hager, 1972) or species-specific response tendencies (Bellis, 1970) in the acquisition and performance of discrimination tasks. Rats have a strong predisposition to alternate responses among spatially distinct choices, even though there is no differential reinforcement contingent upon this behavior (see Douglas, 1966 for a review of the literature). The high choice accuracy on the first few days of formal testing in the radial arm maze may reflect a nonspecific tendency to alternate choices that is independent of the training received during shaping. Alternatively, the initial choice accuracy may have been developed by the shaping, but, because formal testing did not begin until after shaping was completed, this development would have been overlooked. In order to obtain a better estimate of the extent to which animals are predisposed to perform the task correctly and of the extent to which training influences this predisposition, a 17-arm radial maze was constructed of hardware cloth and was placed on the floor. Animals readily walked through the arms of this apparatus so that no shaping was necessary, and performance could be measured on a daily basis from the first day in the apparatus.

**Method**

**Subjects.** The subjects were six naive albino rats, 300-350 g at the start of testing. They were housed in individual animal cages in the colony room and had never entered the testing room prior to the experiment.

**Apparatus.** The apparatus was a 17-arm radial maze constructed of 0.5-in. hardware cloth. Each arm had 8-cm-high sides and a 6.5-cm-wide top. The outside end of each arm was closed by hardware cloth and contained a small dish in which food was placed. The inside end of each arm was attached to a circular screen of hardware cloth 30 cm high which prevented the animals from climbing out of the center. Each arm was 69 cm long, and the center area was 87 cm in diameter, the same dimensions as in Expt 1. The apparatus was placed on the floor of the same testing room used for the maze in Expt 1.

**Procedure.** Animals were deprived of food to bring body weights to 85% of their adult level. On each day of testing, one 190-mg Noyes food pellet was placed in the food cup at the end of each arm. The animal was placed in the center of the apparatus and was allowed to choose freely among all arms until at least 17 choices had been made, meaning that either all the pieces of food had been obtained or that a total of 20 min had elapsed. There was no shaping procedure; the first day of testing was also the first day of data analysis. Testing was continued for a total of 26 days.

**Results**

When placed in the apparatus for the first time, animals usually ran directly to the end of an arm and were somewhat hesitant in moving about. They rarely passed directly across the center area of the apparatus, but stayed close to the entrance of the arms. When food pellets were encountered, they were usually eaten, but every rat left some pellets uneaten even though its nose had passed within a few centimeters of the pellet at the end of the arm. During the next several days, the animals explored the apparatus without hesitation and ate all food pellets.

Choice accuracy is summarized in Fig. 4. On the first day of testing, the mean number of different arms chosen in the first 17 choices was 12.6, with a range from 9 to 14. There was no systematic change in choice accuracy for about the first 6 days, after which there was a steady increase, so that at the end of testing there was a mean of 15 different arms chosen in the first 17 choices. Every animal performed better on the last day of testing than on the first day. The right hand ordinate presents the probability expected by chance of each of the outcomes on the left-hand side. These probabilities
were calculated from formula 3.4 in Feller (1950, p. 69) for an “occupancy” problem, i.e., the probability of distributing \( r \) objects in \( n \) locations with \( m \) locations left vacant. The probability of 17 correct responses in the first 17 choices is \( .43 \times 10^{-4} \), the probability of 16 in the first 17 is \( .58 \times 10^{-4} \), etc. An important point to realize is that a small increase in the number of correct responses (on the left-hand ordinate) reflects a much more substantial increase in choice accuracy (on the right-hand ordinate). For example, the expected value on the basis of chance performance is about 11 different arms within the first 17 choices. The chance probability of choosing 12 or more different arms within the first 17 choices on any given day decreases to .33; of choosing 13 or more to .11; 14 or more to .02; 15 or more to .017, etc. Although the increase in the number of correct choices from 12 to 15 seems relatively small, the decrease in the chance probability of this performance is marked, reflecting a major increase in the accuracy of performance.

Discussion

Rats tested on their first day in the apparatus chose an average of 12 different arms in the first 17 choices, a value which was very close to that expected by chance. Performance remained at a near-chance level for about eight days, after which it consistently improved during the next 20 days to an average of 15 correct responses within the first 17 choices. There are three important results from this experiment. First, initial performance was at chance levels, indicating that the higher accuracy seen during the first days of testing on the elevated maze resulted from the shaping procedure used there. Second, terminal performance in the floor maze was as good as that on the elevated maze, demonstrating that changing the type of apparatus had no noticeable effect on choice accuracy. Third, development of accurate choice behavior took place over an extended period of time and required about 20 days to reach asymptotic levels, demonstrating an important contribution of learning to final performance accuracy.

The poor performance during the first few days of testing was surprising in light of rats’ strong tendency to alternate spontaneously among spatially distinct alternatives in situations as diverse as the standard T maze (Douglas, 1966) and a seminaturalistic environment containing several different piles of food (Olton, Walker, Gage, and Johnson, 1977). In both of the above cases, animals were given substantial experience in the apparatus prior to testing for alternation. The absence of alternation in the present paradigm (as indicated by chance performance on the first several days) might be caused by either the increased number of alternatives or the animal’s lack of familiarity with the stimuli in the testing situation. The present experiment does not distinguish between these explanations. It
does provide information about the effects of the shaping procedure in previous experiments, demonstrating that a substantial amount of learning about either reward contingencies or environmental stimuli took place during shaping.

EXPERIMENT 4

Animals in all the previous experiments exhibited two general response tendencies, consistently turning clockwise or counterclockwise when entering the center platform after choosing an arm, and skipping at least one but usually not more than four arms before making their next choice. These response tendencies would tend to simplify the task, at least on the first five choices or so, because they would ensure that the rats would not repeat an already chosen arm until it had completed one circuit around the apparatus. Once the animals reached their starting point, such a procedure would probably not aid choice accuracy to any substantial extent (unless animals regularly chose in a fixed sequential pattern), because chosen arms would be scattered throughout the apparatus. Nonetheless, the question remains as to the extent that these response tendencies might influence either the general accuracy of performance or the analyses used to describe the characteristics of the spatial memory. To answer this question, guillotine doors were placed on the apparatus, and the animal was confined for about 15 sec after every choice in order to interfere with these and any other ongoing response tendencies.

Two additional analyses were conducted to obtain more information about the distribution of choices in the confinement procedure. The first considered only correct choices. In a series of experiments with a multiple-arm maze, Lachman reported that rats tended to choose correct arms maximally distant from their previous choice (Lachman, 1963, 1966, 1969; Lachman & Brown, 1957). A similar result was reported by Douglas, Mitchell, and Kentata (1972) in a two-choice spontaneous-alternation procedure. To determine if the same process was taking place here, the spatial distance between each correct choice and the immediately preceding choice was calculated in terms of the number of intervening arms. The second analysis considered only errors. Olton and Samuelson (1976) found that, when errors were made in the eight-arm radial maze, they were distributed randomly with respect to the remaining correct arms, suggesting that the errors did not result from generalization between correct and incorrect arms. The same analysis was conducted here.

Method

Subjects. The subjects were the six male albino rats previously trained on the floor version of the 17-arm elevated maze in Expt 3. They were maintained under the same conditions as in Expt 1.
Apparatus. The apparatus was the same as in Expt 1, except that a circular 30-cm-high wall was placed around the outside edge of the center platform just inside the entrance to the arms. In front of each arm a 9 × 9-cm hole was cut into the barrier, and a guillotine door was constructed to block access to the hole.

Procedure. Animals were first trained for 15 days without the guillotine doors on the apparatus and were then shaped for seven days to the general procedure of being confined after each choice. They were then tested for 10 days with a 10–15 sec confinement after each choice. The animals were placed in the center of the apparatus with the guillotine doors closed. The doors were opened and, while the animal was on an arm making a choice, the doors to all the other doors were closed. When the animal returned to the center platform, the guillotine door to the chosen arm was closed and all doors remained down for 10–15 sec. All doors were then raised, and the process was repeated until all 17 pieces of food had been obtained or 20 min had elapsed.

Results

During the 10 days of testing with the animals confined after each choice, the mean number of correct responses within the first 17 choices was 15.1, a value slightly higher than that reported for Expt 1. More important, an analysis of response choices indicated that the confinement procedure effectively disrupted the response patterns characteristic of performance in Expts 1–3. This analysis considered all choices in a day except the first. The arm chosen on each choice was numbered 0. Arms clockwise to this arm were consecutively numbered from 1 to 8, while arms counterclockwise were consecutively numbered from -1 to -8. The relationship of each choice to the immediately previous choice was determined by summing these scores over all choices and all days and calculating the relative probability of each score from -8 to +8. To the extent that the confinement procedure was successful in blocking the response patterns of Expt 1, the distribution of choices from -8 to +8 should be equal. To the extent that the response patterns observed in Expt 1 still persist, the +2, +3, +4, -2, -3, -4, categories should have proportionally more choices than any other.

The results of this analysis for the first 10 days of testing (when the guillotine doors were not present) and for the 10 days of testing when the animals were confined after each choice are presented graphically in Fig. 5. During the 10 days without confinement, the response tendencies described in Expt 1 are clear; 92% of all choices were made to the eight arms closest to the arm just chosen, while only 8% were made to the other eight arms. During the 10 days with confinement, the pattern was markedly different, with the relative percentage being essentially the same for all arms except the one just chosen. These results were characteristic of individual rats as well as of the group as a whole. The confinement procedure was successful in eliminating the turning tendencies of the animals in the nonconfinement procedure.

The analysis of serial-order effects described in Expt 1 (see Eq. (2) and Fig. 2) was also conducted here. There was no relationship between the probability of making an error by repeating a previously correct choice and the sequential position of that correct choice in the day. Thus the small recency effect observed in Expt 1 was not found in the present procedure.

To determine if rats tended to choose correct arms maximally distant from their previous choice, the spatial distance between each correct choice (except the first) and the immediately previous choice (correct or incorrect) was measured in terms of the number of intervening arms. The arm previously chosen was numbered 0. The two arms adjacent to it on either side were numbered 1, the two arms adjacent to those were 2, etc., to the two arms most distant, which were numbered 8. The observed spatial distance relative to the expected spatial distance was calculated according to the formula:

\[
\begin{align*}
\text{if } SD_{\text{exp}} > SD_{\text{exp}} & \quad \frac{SD_{\text{obs}} - SD_{\text{exp}}}{8 - SD_{\text{exp}}} \\ 
\text{if } SD_{\text{obs}} < SD_{\text{exp}} & \quad \frac{SD_{\text{obs}} - SD_{\text{exp}}}{SD_{\text{exp}} - 1}
\end{align*}
\]
where \( SD_{\text{obs}} = \text{arm number of correct choice} - 0 \), and \( SD_{\text{exp}} = \frac{\text{number of correct choices}}{\text{number of possible correct choices}} \). The result of the formula is a percentage maximum performance score. Scores greater than 0 indicate more spatial distance between choices than expected by chance (Lauchman's observation, with a score of 1.0 indicating the maximum possible distance \( SD_{\text{obs}} = 8 \)). Scores less than 0 indicate less spatial distance between choices than expected by chance, with a score of -1.0 indicating the minimum possible distance \( SD_{\text{exp}} = 1 \). The mean and range of scores for animals in the confinement procedure was .03 (-.15 to .23), indicating that correct choices were distributed randomly with respect to the immediately previous correct choice. [In the nonconfinement procedure, all scores were negative (range: -.36 to -.82), demonstrating that the rats chose correct arms closer to their immediately previous choice than expected by chance.]

To determine if errors tended to be made close to correct arms, the arm chosen on the error was divided by the two immediately adjacent arms were 1, etc., to the two most distant arms which were numbered 8. The observed spatial distance between the error and each of the possible remaining correct choices was compared to the expected spatial distance by the formula:

\[
SD_{\text{obs}} - SD_{\text{exp}}
\]

where \( SD_{\text{obs}} = \frac{\text{number of each possible correct choice}}{\text{number of possible correct choices}} \) and \( SD_{\text{exp}} = \frac{\text{number of arms}}{\text{number of arms}} = \frac{21 + 2 + \ldots + 8}{16} = 4.5 \). Scores less than 0 indicate that errors were closer to correct arms than expected by chance, with a score of -3.5 (1 to 4.5) indicating an adjacent arm. Scores greater than 0 indicate that errors were farther away from correct arms than expected by chance, with a score of 3.5 (8 to 4.5) indicating the farthest possible arm. The mean and range of scores for rats in the confinement procedure was .9 (.4 to 1.3), indicating that, when the rats made errors, they did not tend to choose arms close to ones that were correct. [In the nonconfinement procedure, the mean score was .3 and the range was -.2 to .8.]

Observation of the animal's behavior indicated that they were often in front of an arm that was correct when the guillotine doors were opened, and that they were more likely to enter the arm they were in front of if it was correct than if it was incorrect. Quantitative estimates of these tendencies were obtained by calculating the following for each choice: (a) the probability of standing in front of a correct arm, corrected for the chance probability of standing next to a correct arm and expressed as a percentage maximum performance score as in the transformed probability of a correct response; (b) the relative conditional probability of going to the arm by which the animal was standing if that arm was incorrect. Results of these analyses indicated, respectively: (a) The mean probability of standing in front of a door to a correct arm when the guillotine doors were raised was .45 and was consistently greater than chance, even on the last few choices of the day. (b) The mean probability of responding to the arm by which the animal was standing if the arm was correct was .92, a value that was significantly greater than 0 and characteristic of all choices during the day. (c) The mean probability of responding to the arm by which the animal was standing if the arm was incorrect was .18, a value significantly less than that reported for (b) above and characteristic of all choices during the day.

For readers who wish to perform additional analyses on the data, the results from the last 10 days for animals in the confinement procedure are presented in the Appendix. As before, the daily choices for each animal are indicated, with the number indicating the arm chosen.

**Discussion**

The confinement procedure used in the present experiment was successful in blocking the tendency of animals to choose preferentially close to the arm just chosen, making it possible to determine to what extent the results of Expt 1 were influenced by these response variables. The first question was whether the response tendencies in Expt 1 were a "strategy" in the sense that they were "of great importance ... to the undertaking of a planned ... occurrence" (Webster's, 1971). Since these tendencies were eliminated in the present experiment while choice accuracy was unaffected, the results suggest that they are more accurately characterized as convenient rather than strategic behavior for the rats.

The other questions concerned the characteristics of spatial memory as described in Expt 1. The probability of a correct response was unaffected by confinement, indicating that, as the number of arms to be remembered increased, the accuracy of choices decreased. The relative probability of repetition per opportunity was no longer a function of the sequential position of the original choice, indicating that the small recency effect observed in Expt 1 and in Olton and Samuelson (1976) probably did result from response tendencies. Such an outcome is, of course, reasonable, because the major source of the recency effect was observed on the last few choices of the day; the response tendencies in the nonconfinement procedure would make the animal unlikely to return to the place of the last few choices before the test ended. The conclusions of Expt 1 and those of the previous eight-arm radial maze experiments, with respect to the overall accuracy of performance, the unimportance of response chains or response patterns, and the decline of choice accuracy during each test, are firmly supported by these results. The suggestion of a recency effect is not.

The apparently random spatial distribution of responses poses a substantial difficulty for any detailed account of the animals' choice
behavior. On any given choice, the arm chosen was more likely to be correct than incorrect, with the probability of a correct choice decreasing as the number of prior choices increased. But the particular arm entered on any given choice seemed to be chosen randomly. On correct choices, the mean spatial location of the arm chosen relative to the previous choice was almost exactly the value expected by chance. On incorrect choices, the mean spatial location of the arm chosen relative to the remaining correct choices was, in no case, less than the value expected by chance. These results are surprising in light of the strong alternation tendency found in two choice mazes (see Douglas, 1966) and in a radial arm maze similar to the one used here (Lachman, 1963, 1966, 1969; Lachman & Brown, 1957). But, in each of the above experiments, the animal always approached the choice point from the same direction, a factor which may have contributed to the tendency to choose arms maximally distant from the one just chosen. In any case, the confinement procedure used here, the spatial location of any particular choice seems to be unimportant compared to the spatial location of the previous choice, and the variables that influence which one of the possible alternatives will be chosen cannot be specified at the present time.

The results of the three probability analyses provide more detailed information about the spatial and temporal course of discrimination with the confinement procedure. In spatial paradigms, evidence of learning often appears independently in start arms, choice points, and goal arms (Hull, 1933; Maller, 1961; Olton, 1974). With the confinement procedure, some of the discrimination process appeared to take place when the guillotine doors were closed as indicated by the high probability of standing next to a correct arm. Successful discrimination still took place after the guillotine doors were opened, as indicated by the difference between the probability of responding to a correct arm and the probability of responding to an incorrect arm, and this discrimination was highly accurate. When the guillotine doors were first introduced, all animals dined through the nearest door as soon as it was raised in an almost compulsive fashion. This behavior gradually decreased as training proceeded, but was always present to some extent and may have been responsible for the probability of responding to an incorrect arm being so great. If this conjecture is correct, continued training might have further reduced this response tendency and increased the accuracy of discrimination after the guillotine doors were raised by decreasing the probability of responding to an incorrect arm. In any case, the probability analyses indicate that successful discrimination between correct and incorrect arms took place both while the guillotine doors were closed and after they had been raised.

The confinement procedure resulted in animals completing approximately 10 choices in the time usually required to make 17. Yet, choice accuracy on choices 10-17 was no worse in the present paradigm than in Expt 1. These data indicate that choice accuracy declined as a function of choices rather than time and provide additional support for the conclusion that the decrease in the probability of a correct response across choices results from interference in the memory store rather than from decay of the memory trace (Olton and Samuelson, 1976).

**GENERAL DISCUSSION**

Rats performed well in the 17-arm radial maze, making an average of more than 14 correct responses in the first 17 choices without relying on an intramaze marking system, a general algorithm, or a response chain. Even on the seventeenth choice, when the animals had to remember approximately 13 previous correct choices, performance was consistently above that expected by chance. This marked accuracy again demonstrates the efficacy of "place learning" in directing animal choice behavior. But this result, although in need of "rediscovery," has been sufficiently well documented to need little further support (see literature review in the introduction). Thus, the major contribution of the present series of experiments is not in providing additional evidence to support the influence of spatial cues, but in introducing a new experimental paradigm which can be applied to currently important questions about animal cognitive processes, particularly the nature of working memory. The three issues addressed here were: (i) the capacity of the working memory, (ii) the relative contributions of species-specific predispositions and learning to performance, and (iii) the spatial distribution of choices in a confinement procedure which interrupted the response tendencies observed in the normal testing paradigm. Each of these points will be discussed in turn.

In the previously reported experiments with an eight-arm maze (Olton & Samuelson, 1976), rats performed almost perfectly, making an estimate of the limits of working memory very difficult. In the present paradigm, although rats still performed well, they did have difficulty locating the last few pellets of food on each test, and the probability of a correct response decreased to about .40 on the seventeenth choice. If the probability of a correct response curve in Fig. 1 is extrapolated, choice accuracy would reach chance levels at 25-30 choices, suggesting that this may be the limit of rats' working memory in this paradigm.

Following shaping, choice accuracy on the first few days of training was substantially greater than expected by chance. This initial choice accuracy might have resulted from learning about the task during the shaping process or from a general predisposition not to repeat choices. Rats have a strong tendency to alternate choices among equally rewarded alternatives (see Douglas, 1966; Olton et al., 1977), and species-specific predispositions may have an important influence in many types of discrimination tasks (see Seligman & Hager, 1972). In Expt 3 in which animals without prior shaping were tested, choice accuracy on the first few days was
better than expected by chance. These results are important because they demonstrate that substantial learning takes place during the shaping process normally used prior to formal testing. Thus, general species-specific predispositions seem to have little influence on initial choice accuracy.

The confinement procedure in Exp. 4 provided several important pieces of information. First, confinement did not affect choice accuracy, again demonstrating that response patterns are not important for accurate performance. Second, no recency effect was observed with confinement, suggesting that working memory in this paradigm has no serial order and that the slight recency effect reported in previous experiments was an artifact of the turning tendencies exhibited by animals in the free-running situation. Third, the spatial distribution of responses among the arms was essentially random, with the exception that animals tended not to return to incorrect arms. Thus, the variables that influence which particular correct arm will be chosen on a correct choice and which particular incorrect arm will be chosen on an error remain unknown. Fourth, the probability analyses provided evidence that accurate discrimination took place both in the center platform when the guillotine doors were closed and also at the entrance to the arms when the guillotine doors were open.

In summary, these experiments confirm the results reported previously by Olton and Samuelson (1976) and demonstrate the usefulness of spatial paradigms in assessing the characteristics of working memory. They also provide additional information about the capacity of working memory, the importance of learning, and the spatial organization of choices in this task.

(See Appendix, pp. 311–313.)
The first part of the appendix presents daily choice data for six animals in Expt 1. Days 21–30, which were tested without confinement between choices. The second part presents the daily choice data for the six animals in Expt 4 during the last 10 days of testing when they were confined to the center platform after each choice. In all cases, only the first 27 choices are presented to conserve space. The number indicates the arm chosen. Only the first choice of each arm was rewarded.

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Choice Behavior of Perches

DAVID S. OLTON, JOHN W. COLLISON, AND CRAIG P. WERZ

The Johns Hopkins University

The experiments reported here were designed to study principles drawn from appetitively motivated animal behavior and laboratory apparatus might also appear in a more naturalistic context. Food-deprived birds in a naturalistic situation area. Choice behavior after finding food was also analyzed. In all cases, not finding food was sufficient to direct subsequent search behavior. The number of days food was in one location and the number of days food was in another location results indicate that the rats' search strategies and distribution in ways that are predictable.

A fundamental discrimination problem arises in the experiments. In particular, consider an animal's choice in sufficient quantity to provide a constant food supply. How are searches be directed? One strategy is to leave the site of the initial find. This is appropriate if food sources tend to be congregated, so the probability of finding additional sources is higher. If the initial find is appropriate, then the probability of finding additional sources is lower. Examples of both these strategies are observed. In the experiment with blackbirds, direct subsequent searches in the vicinity of the first food source was observed.

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