

Within-Trial Dynamics of Radial Arm Maze Performance in Rats

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The behavior of rats while solving a 12-arm radial maze was investigated using measures of response bias, choice latencies, and behavioral organization. Response bias decreased as a function of choice number, while the amount of time spent on the center platform between choices increased substantially during the last few choices. This increase in time between choices was largely accounted for by increases in investigatory behavior in the area of the doors leading to the arms. These data indicate that the processes involved in radial maze performance change over the course of each trial. As the choice sequence progresses, there is an increasing reliance on the use of information in memory, and a corresponding decrease in the use of response algorithms. In addition, the mean time taken to run down the chosen arm was shorter for correct choices than for incorrect choices, suggesting that arms are sometimes chosen despite a lowered expectation of finding food. © 1986 Academic Press, Inc.

Since the report of Olton and Samuelson (1976), the radial maze has become a popular preparation for the study of animal memory. In this task, an animal is placed on an elevated platform that has a number of runways (e.g., eight) radiating from it at equal angles. The animal consumes a small number of food pellets from the end of each arm, returning to the center platform between choices. Revisits to arms during a trial are defined as errors, since food is never available on previously visited arms. Thus, subjects must discriminate arms chosen previously during a trial from those that still contain food in order to avoid making errors.

The radial maze has been used to investigate issues such as the structure of "spatial memory" (Suzuki, Augerinos, & Black, 1980), the cues used

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in performing spatial tasks (Mazmanian & Roberts, 1983), memory coding (Cook, Brown, & Riley, 1985), proactive interference (Roberts & Dale, 1981), retroactive interference (Roberts, 1981), the effects of retention intervals (Beatty & Shavalia, 1980), neurophysiological mechanisms of memory (Olton, Becker, & Handelmann, 1979), and ecological aspects of spatial ability (Bond, Cook, & Lamb, 1981).

While a great deal of effort has been directed at understanding the processes that allow rats to successfully complete the radial maze, little attention has been paid to the dynamics of those processes, i.e., how they change during the course of each trial. The typical measures used in studies of radial maze performance result in a single index of choice accuracy for each trial. With the exception of analyses of serial position curves (Cook *et al.*, 1985; DiMattia & Kesner, 1984; Kesner & Novak, 1982; Roberts & Smythe, 1979), these measures are not designed to reveal changes in behavior or psychological processes that might occur during the series of choices that constitute each trial.

The present experiment explored the possibility that more direct measures of behavior in the radial maze might reveal changes in the mechanisms controlling choices over the course of each trial. The first was a measure of response bias. Typically, the animal chooses freely from among the arms, allowing the possibility that choices are based, in part, on response biases or algorithms (Bond *et al.*, 1981; Yoerg & Kamil, 1982). The amount of information needed to avoid incorrect choices could be reduced by visiting arms in a consistent, systematic manner. For example, if a rat were to turn left and enter the adjacent arm following each choice, it could perform perfectly without having to encode any information about previous choices. Although some experiments have failed to reveal such strategies (e.g., Olton & Samuelson, 1976), others have found conditions under which response biases are prevalent (Yoerg & Kamil, 1982).

In the present experiment, the degree of nonrandomness in the behavior of the rats was indexed using the information theory statistic H (cf. Attneave, 1959). Given a set of events, in this case the set of responses of each rat, one can determine the number of "bits of information" (H) which would be required to uniquely specify that set (cf. Suzuki *et al.*, 1980). The more redundancy there is in the set (i.e., the more the rat tends to respond in the same way), the less information is required to describe the behavior. Thus, if a rat has a consistent turning bias, few bits of information would be required to describe its behavior. If its turning behavior includes a large degree of uncertainty, then more information would be required to describe it. Calculation of H for each choice number allowed the stereotypicality of choice behavior to be measured as a function of choice number.

Temporal aspects of behavior were also measured. For each choice, the amount of time spent (a) in the center of the maze prior to entering

the arm and (b) on the arm was measured. As the animal depletes food from the arms, the probability of choosing a correct arm by chance decreases. Consequently, the difficulty of finding a correct arm increases as a function of choice number. This increasing difficulty might be reflected by increases in the amount of time required to discriminate correct (unvisited and baited) arms from incorrect arms. The measurement of time spent in the center between choices (center time) and time spent on the arms (arm time) may also help determine where in the maze this discrimination takes place. If the discriminations involved in successful performance occur on the center platform, then center time would be expected to increase over the course of each trial to a greater extent than arm time. Likewise, if rats use information available while they are on the arms to guide subsequent choices, then a greater increase in time spent on the arms than in time spent on the center platform would be expected.

Successful performance in the radial maze depends on the use of extra-maze cues (Mazmanian & Roberts, 1983; Olton, 1978; Olton & Collison, 1979; Suzuki *et al.*, 1980). While the exact manner in which such cues are used is not well understood, presumably a comparison of the cues associated with different arms of the maze to information represented in memory is involved. Thus, an index of the relative occurrence of behaviors corresponding to visual and/or olfactory orientation might provide information about the extent to which memory is involved in choice behavior over the course of each trial. Casual observation of rats' behavior during previous experiments performed by the authors and during the early phases of the present experiment suggested several behaviors that might be involved in the acquisition of information from extra-maze cues, in that they all involve orientation toward objects or areas external to the maze. One, termed "door investigation," involved active examination of the area near the entrances to arms, including visual orientation toward the end of the arm. A behavior that was termed "cracking" consisted of the extension of the snout through the "crack" between adjacent arms and visual orientation toward the floor beneath the maze. "Rearing" and "open sniffing" involved standing on the hind legs and were accompanied by orientation toward extra-maze cues.

If changes in center time or arm time over the course of each trial were due to an increasing reliance on memory to guide choices, then the proportion of center time or arm time spent engaged in these orientation-related behaviors would be expected to increase. If, on the other hand, center time or arm time increase because of motivational changes (such as satiation) or because of an increased difficulty in consuming food pellets, then the proportion of time spent engaged in behaviors other than these would be expected to increase: for example, time spent grooming or simply stopping in the center of the maze or time spent eating on the

arms. During a second phase of the present experiment, the time spent engaged in six categories of behavior that occurred in the center of the maze was recorded and examined as a function of choice number. During a third experimental phase, the behaviors occurring on the arms of the maze were measured in an attempt to understand any increases in time spent on the arms as a function of choice number.

Observation of rats in the radial maze by the authors also suggested the possibility that incorrect choices are often associated with slow running speeds as the rat travels from the center platform to the food cup. In a fourth phase of the experiment, this possibility was formally investigated by measuring the amount of time taken to run from the choice point to the food cup. Measures of running speed have previously been used to infer reward expectation (e.g., Capaldi & Verry, 1981; Hulse, 1978; Jensen & Rey, 1969). Running more slowly to incorrect arms than to correct ones might indicate that arms are sometimes chosen despite a lowered expectation of reward. Another possible explanation for slower latencies when errors are made would be that the absence of food in the cup is simply detected (e.g., by sight or smell) as the rat runs down the arm. A test of this possibility was included. During a single probe trial, only half of the arms were baited prior to the trial. If running speed is affected by sensory cues corresponding to the absence of food in the cup, then latency to run to an empty, but novel (correct) arm should be longer than latency to a baited, novel arm. If longer latencies during incorrect choices are a function of previous visit(s) rather than the absence of food, then latency to novel unbaited arms should be the same as latency to baited arms.

To summarize, the experiment was divided into four phases. During the first phase, time spent on the center and arms of the maze were measured as a function of choice number. The degree of response bias was also measured as a function of choice number. The second and third phases were concerned with the behavioral correlates of changes in center and arm time. The final phase included measures of the time taken to run from the choice point to the food cup.

METHOD

Subjects. The subjects were 10 Sprague-Dawley albino rats, six males and four females. The rats were maintained at 80–85% of their free-feeding weights in a room with a 12:12 LD cycle and free access to water.

Apparatus. The apparatus was a 12-arm radial maze, elevated 0.61 m above the floor. It was constructed out of wood and painted flat white. Twelve arms radiated out at equal angles from a circular center platform that was 41 cm in diameter. Each arm was 80 cm long and 10 cm wide. The entrance to each arm was through a 7.5-cm hole, cut into a thin

metal wall, 12.5 cm in height, that surrounded the center platform. Entrance to the arms was controlled by a cylindrical guillotine door that opened all the arms simultaneously when raised. Barriers, 12.5 cm in height and 26 cm in length, were attached to the clockwise side of each arm where it met the metal wall, to ensure that the animals returned to the center platform between choices. Stainless-steel food cups, located at the end of each arm, were 11 cm in diameter and 1.5 cm deep.

The maze was located in a well-illuminated room with a variety of extra-maze objects, such as cages, a furnace, a sink, a white panel, and chairs. A large black plastic sheet divided two sides of the experimental area from the rest of the large room.

Temporal data were recorded with an Esterline–Angus event recorder (Model A620X). Events were timed by depressing hand-held buttons. The temporal data were transcribed with 0.5-s accuracy.

Training. Rats were shaped to enter the arms by placing food pellets (45-mg Noyes) along each arm and two additional pellets in each food cup. The rats were allowed to explore the maze for 20 min or until all the food was consumed. After several trials, the rats spontaneously visited the food cups at the ends of arms and the shaping pellets were no longer used.

Twenty additional training trials were conducted. One trial per day was conducted during the first 4 h of the dark phase of the LD cycle. On these training trials, the rats were placed in center of maze, oriented in a random direction. Approximately 10 s later, the guillotine door was raised allowing the rat to make choices. Trials ended when either 20 choices, 20 min, or 12 correct choices had occurred. An arm was considered chosen when the rat's nose crossed the end of the barrier that was attached to each arm (i.e., 26 cm from the entrance to the arm). A correct choice was defined as the first visit to an arm during a trial. Each arm was baited with two pellets.

Phase 1. Following training, the rats were tested for 14 trials, during which the sequence and accuracy of each choice, the amount of time spent on each arm and in the center of the maze between each choice, and the direction of the turn made upon exiting each arm were recorded. In all other respects, these sessions were conducted in the same manner as the training sessions. One experimenter recorded the sequence and direction of turns from ground level, about 3 m from the maze. Upon exiting an arm, the rat's direction of turn was recorded as either clockwise, counterclockwise, or neither (directly toward the opposite arm). The last category occurred very infrequently. The maze was divided into two areas and the amount of time spent in each was recorded by a second experimenter, located about 2.5 m above and to one side of the maze. "Center time" was defined as the time spent on the center platform and on the portion of the arms between the central platform and the end of

the barriers before the choice was made. "Arm time" was defined as the time spent on the portion of the arm beyond the end of the barrier between passing the end of the barrier and returning to the area defined as the center.

Phase 2. During Phase 2, behavior occurring on the central platform of the maze was investigated. The frequency and duration of six behaviors were recorded by depressing buttons during the occurrence of each behavior. The behaviors were defined to be mutually exclusive.

During a preliminary series of four trials, each experimenter recorded behavioral data during two trials for each rat. After each trial, the definition and adequacy of the behavioral categories were discussed in order to maximize interobserver reliability and the completeness of the behavioral description. During the eight experimental trials, one experimenter recorded the behavioral data, while the second experimenter recorded center times, arm times, and the sequence of choices in the same manner as in Phase 1. The assignment of experimenters to these two tasks alternated between trials. The frequency and duration of the following behaviors were recorded:

Door Investigation. Actively examining the entrances to the arms, defined as being within 2.5 cm of the door. This included sniffing or looking through the entrance. A frequently observed pattern consisted of the rat moving from door to door and looking through each in turn.

Cracking. Extension of the head into the open space (crack) between the arms and breaking the horizontal plane defined by the maze arms with the nose. This behavior was observed both on entering and exiting arms. The rat appeared to be examining the floor of the room.

Rearing. Standing on hind legs with both forepaws off the floor of the maze. This behavior usually occurred near the wall of the center platform with one or both forepaws on the wall.

Grooming. Any grooming activity, the most frequent of which were face washing (rubbing the face with the forepaws) and flank grooming (scratching or biting the belly or flank).

Center Sniffing. Sniffing the center platform in the area not defined as door investigation (i.e., the nose was close to the floor of the maze and the whiskers moved while the rat was at least 2.5 cm away from the wall).

Stopping. A state of motionlessness that occurred when the rat was not engaged in any category of behavior. This category was invoked approximately 1 s after the animal stopped moving. Stopping occurred most frequently while exiting an arm and prior to completely entering the center platform. Chewing was sometimes observed during this time.

Phase 3. This phase lasted for eight trials, with each experimenter recording behavioral data four times during alternate trials. The procedure was identical to Phase 2, except that the behavior of the rats on the arms was recorded and the behavioral categories were tailored to the behavior of the rats on the arms. The categories were derived in the same fashion as in the last phase. During four trials conducted between

Phases 2 and 3, the behavior of the rats was observed and appropriate categories were formed.

The behaviors recorded were:

Arm Investigation. Investigatory activity (including sniffing) directed at the surface of the arm or the barrier between adjacent arms.

Eating. Behaviors that occurred while the rats ate the food pellets, such as chewing and food manipulation with the forepaws.

Cracking. Similar to the behavior observed in Phase 2. The rat's nose broke the plane defined by the maze surface. The rat appeared to be examining the floor of the room.

Grooming. Any grooming activity, the most frequent of which were face washing (the rubbing of the face with the forepaws) and flank grooming (the scratching or biting of the belly or flank).

Open Sniff. Rearing and extending the nose while at the end of the arm and sniffing (and looking?) beyond the end of the arm.

Phase 4. The rats were tested for nine trials using the same procedure as in the previous phases, except that the time taken to traverse each arm (running time) was recorded. A timer was started when the snout of the rat crossed the end of the barrier that separated adjacent arms and stopped when its snout crossed the vertical plane defined by the edge of the food cup.

On Trail 5, only half of the arms were baited. These were determined randomly for each rat. This trial was terminated using the same criterion as before, with the first visit to a (baited or unbaited) arm considered correct, and subsequent visits to the same arm considered incorrect.

RESULTS

Phase 1

Accuracy. During the 14 trials of Phase 1, the rats chose a mean of 11.5 correct arms of the first 12 choices (chance = 7.8 arms). The rats completed the maze after a mean of 12.9 choices.

Response biases. The turning behavior of the rats was categorized according to (1) the direction of the turn from the arm that was previously exited (clockwise or counterclockwise) and (2) the number of arms from the previous choice to the choice in question. This resulted in 22 categories of turning behavior; turning clockwise or counterclockwise and travelling from 1 to 11 arms (a small number of choices without a clear direction of turn were excluded). The number of bits of information (H ; cf. Attneave, 1959) required to describe the behavior of each rat during the 14 trials was determined for each choice number (i.e., the ordinal position of the choice within each trial). For each choice number, a maximum of 3.8 bits would be required to describe the behavior of a rat over these 14 trials if its behavior was maximally uncertain, i.e., if it contained no response biases. Figure 1 shows the mean degree of uncertainty as a

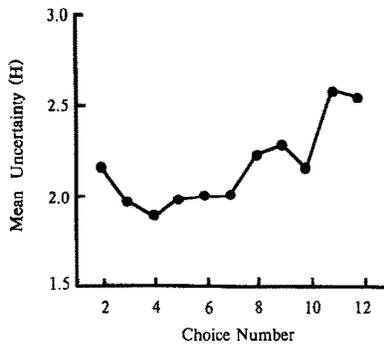


FIG. 1. The mean uncertainty of turning behavior in terms of the number of bits of information (H) required to specify it for the trials of Phase I. Data are shown as a function of the ordinal position of the choice made following each turn.

function of choice number; lower values of H indicate greater response bias. A repeated measures analysis of variance (ANOVA: Choice Number \times Rats) was performed using the value of H for each rat at each choice number. A significant effect of choice number was found [$F(10, 90) = 2.9, p < .01$]. There was a greater degree of uncertainty in the behavior of rats later in the choice sequence than earlier, indicating that response biases were more prevalent during early choices.

To examine whether response biases affected choice accuracy, the correlation between the degree of bias of a rat and its accuracy was calculated. The degree of bias in the choice behavior of each rat (collapsed across choice number) did not covary with accuracy as measured by the mean number correct choices out of the first 12 ($\rho = -.03$, Spearman ρ).

Temporal measures. The mean time spent in the center area and on the arms as a function of choice number is shown in Fig. 2. A repeated measures ANOVA [Location (center vs. arm) \times Choice Number \times

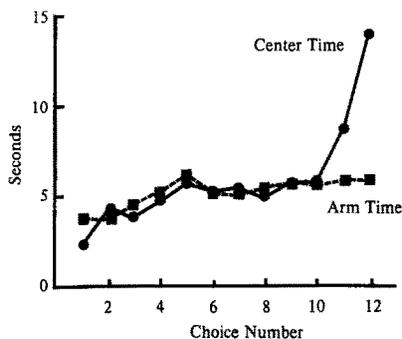


FIG. 2. The mean time spent on the center of the maze and on the arms as a function of choice number during Phase I.

Rats] was performed to determine if the increase in center time over choices was greater than the increase in arm time. It revealed a significant interaction between choice number and location [$F(1, 11) = 7.0, p < .025$] due to a larger increase in center time than in arm time during the last few choices. Separate analyses of center time and arm time revealed that both indices varied significantly with choice number [center time, $F(11, 99) = 10.9, p < .001$; arm time, $F(11, 99) = 6.9, p < .001$].

Phase 2

For efficiency of presentation, data presented from Phases 2 and 3 are restricted to three sets of two choices each (the 1st and 2nd, 6th and 7th, and 11th and 12th). The upper left panel of Fig. 3 shows center time

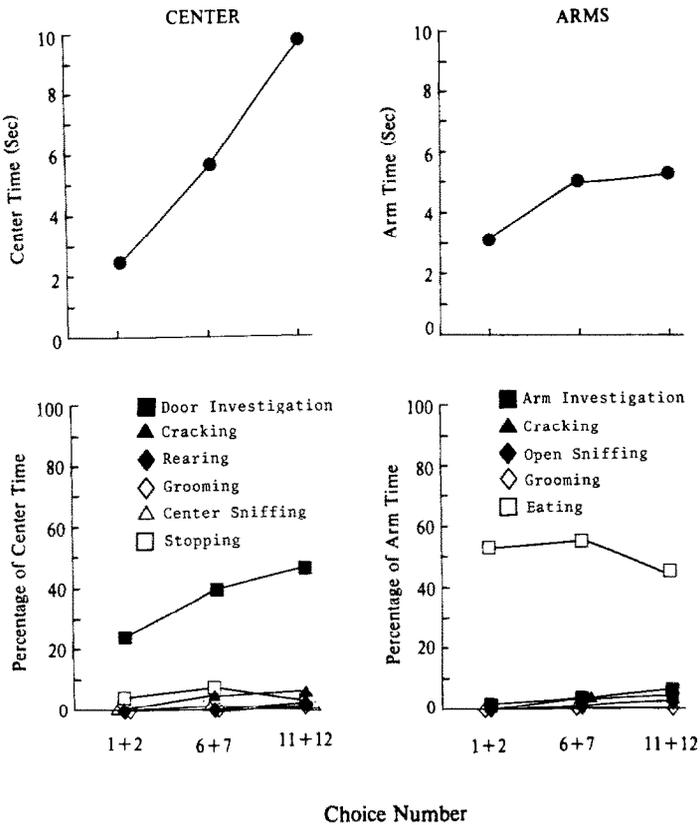


FIG. 3. The mean time spent in the center of the maze (upper-left panel) and the percentage of the time spent engaged in the behaviours measured (lower-left panel) during the early, middle, and late choices in Phase 2. The corresponding data from Phase 3, in which the amount of time spent on the arms and the percentage of time spent engaged in various behaviors on the arms was measured, are shown in the upper-right and lower-right panels, respectively.

and the lower left panel shows the proportion of center time that was spent engaged in the various behaviors during these pairs of early, middle, and late choices. Center time was again found to increase as a function of choice number. The center time not accounted for by the behavioral measures consisted almost exclusively of the time spent moving from one arm to another in a manner that was not regarded by the experimenter as part of a door investigation episode. The majority of center time was not accounted for by the behavioral measures used in this experiment, because the typical pattern was for the rat to proceed straight from one arm to the next. For all 10 animals, the recorded behavior which was most prevalent throughout the trials was door investigation.

Nine of 10 rats spent a greater amount of time and a larger proportion of center time engaged in door investigation during the middle pair of choices than during the early pair ($p < .05$, sign test) and 9 of 10 spent a greater amount of time and a larger proportion of choice time door investigating during the late pair than during the middle pair ($p < .05$).

Phase 3

The upper right panel of Fig. 3 shows the mean arm times during Phase 3. The lower right panel shows the proportion of arm time that was spent engaged in the various behaviors during early, middle, and late choices of Phase 3. Arm time was again found to increase with choice number. Eating was by far the most prevalent behavior. This was true for all 10 animals ($p < .01$, sign test). While the proportion of arm time spent eating did not increase with choice number, the small increase in arm time was largely due to an increase in the absolute amount of time spent eating [$F(2, 18) = 4.3$, $p < .05$]. Most of this increase occurred between the early and middle portions of the choice sequence. The increase in the amount of time spent eating the food pellets is not reflected in Fig. 3 because of an increase in time spent engaged in unmeasured behavior, such as the time taken to return to the central platform.

Phase 4

Running time for correct choices during the eight trials of Phase 4 in which all arms were baited did not vary as a function of choice number [$F(11, 99) < 1$]. During the eight trials with all arms baited, the rats made a total of 62 errors (93.6% of the first 12 choices were correct). Mean running times for correct and incorrect choices during the eight trials on which all the arms were baited are shown in the left portion of Fig. 4. Mean running times during correct choices to baited and unbaited arms during the probe trial are shown in the right portion of Fig. 4. During the probe trial, running time to correct, unbaited arms did not differ from running time to correct, baited arms. However, of the nine rats that made one or more errors during the other eight trials, eight of

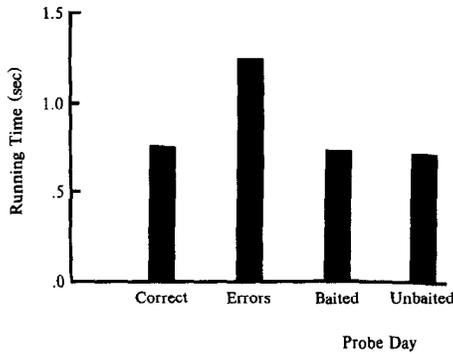


FIG. 4. The mean latency to run from the end of the barrier separating the arms to the food cup (Running Time) during Phase 4. The two leftmost bars show data from correct and incorrect choices from trials in which all arms were baited. The two rightmost bars show data from correct choices during the probe trial, in which only half of the arms were baited.

them had longer mean running times when an incorrect arm was chosen than when a correct arm was chosen ($p < .05$, sign test). Figure 5 shows the distribution of running times for correct and incorrect choices. About half of the errors were associated with running times that were equivalent to running times for correct choices. The other half of the errors, however, were associated with longer running times.

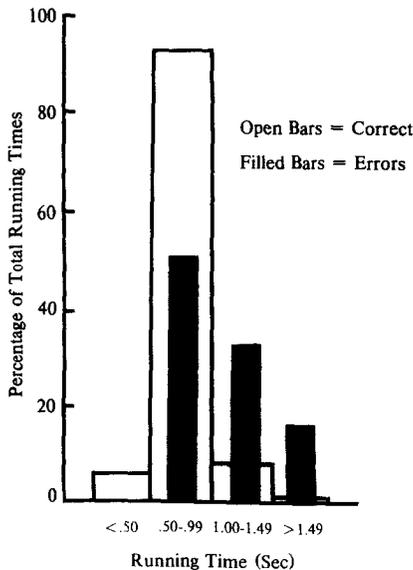


FIG. 5. The distributions of running times for correct and incorrect choices made during Phase 3. Data from the probe trial are not included.

DISCUSSION

The experiment reported in this article demonstrates that complex changes occur in the behavior of rats in the radial arm maze as the choice sequence progresses. During the course of each trial, there is a decrease in the use of response biases and an increase in the time spent in the central arena between each choice. The latter effect can be accounted for by an increase in investigatory activity around the area of the doors. These changes in behavior suggest that the processes determining behavior also vary over the course of the choice sequence.

One reason for a greater reliance on response biases early in the choice sequence may be that a larger number of unvisited arms are available to choose from, allowing response biases to be expressed without reducing choice accuracy. The use of response biases might be encouraged if the bias results in a reduction of the amount of time between food pellet rewards. It is also possible that visiting arms in a systematic manner increases efficiency by decreasing the amount of information that needs to be retained. In the case of most response biases, however, choices made later in the choice sequence cannot be made according to a response bias without seriously compromising accuracy. For example, a response bias often observed was to skip the adjacent arm and visit every other arm. If followed throughout the trial, this would result in a series of errors after the sixth choice. The lack of a correlation between the degree of response bias of the rats and their accuracy indicates that response biases neither facilitate nor inhibit successful performance. Thus, there is no indication that rats utilize the potential benefits of response biases early in the trial or suffer the potential disruptive effects of response biases late in the trial.

The increase in center time during the course of the trial implies a change in the determinants of arm choice that is restricted to the center of the maze. The increase in center time may reflect an increasing reliance on the memorial processes used to discriminate between correct and incorrect arms. The fact that an increase in door investigation can largely account for the change in center time is consistent with this hypothesis. Exploration of the area around the doors in succession was first noted by Olton and Samuelson (1976). This behavior suggests that each arm is treated as a discrete item, and that the familiarity of each arm is evaluated one at a time and in succession. There are at least two possible explanations for the increase in door investigation. One possibility is that more arms need to be investigated before a correct one is found. A second possibility is that more time is required to evaluate whether an arm has already been visited. Such an increase in difficulty of each discrimination might be expected for a number of reasons. For example, there may be a buildup of proactive interference over the course of each

trial (Roberts & Dale, 1981). Alternatively, if rats retrospectively remember each previously chosen arm (Cook *et al.*, 1985), then more memorial representations would have to be compared to each potential choice, in a manner analogous to the memory scanning process described by Sternberg (1969). Such a process has been hypothesized by Ellis, Clegg, and Kesner (1984) to explain increases in choice latencies in a three-arm maze. Regardless of whether the increasing incidence of door investigation is due to an increase in the number of arms investigated before a choice is made or to an increase in the time spent investigating each arm, it indicates an increasing reliance on memorial processes.

While the incidence of behaviors that may be related to choice processes increased in the center of the maze as the choice sequence progressed, there was no evidence for any such increase on the arms of the maze. In fact, the small increase in arm time over the course of the choice sequence seemed to be accounted for by an increase in the amount of time spent eating the food pellets. Such an increase in the time required to consume the pellets makes sense, given the fact that rats typically drink water immediately following their meals (Kissileff, 1969). Perhaps the lack of water in the maze results in an increased difficulty in eating food. It remains possible, of course, that discrimination of previously visited arms from unvisited arms does occur on the arms of the maze. The absence of behavior thought to indicate choice processes does not rule out the presence of such processes. Roberts (1981) and Walker and Olton (1979) have found that direct placement of a rat on the arms of the maze during a retention interval disrupts performance, implying that some information used in making choices is acquired while on the arms. It seems likely, however, that information about the current choice is encoded while the animal is on the arm, while discrimination of previously visited and unvisited arms takes place on the central platform.

Cook *et al.* (1985) recently provided evidence that rats use both retrospective memory (i.e., memory for previously chosen arms) and prospective memory (i.e., memory for anticipated choices) in the radial maze. This hypothesis was based on the finding that a retention interval had the greatest disruptive effect on performance when it was interpolated in the middle of the choice sequence and less of an effect when interpolated either early or late in the sequence. Some comment is in order on the relation between the present data and the findings of Cook *et al.* The present data show that the discrimination of correct choices from incorrect choices takes longer as the choice sequence progresses. Assuming that this additional time reflects an increasing reliance on the use of memory, the present data might be taken as evidence that rats were using retrospective memory, since a larger retrospective memory load near the end of the choice sequence could explain the large increase in choice time and the corresponding increase in choice-related behavior. This

interpretation of the data is consistent with the notion, proposed by Cook *et al.*, that the interpolation of a retention interval in the choice sequence is necessary for the use of prospective memory.

On the other hand, it might be expected that even rats using prospective memory would show an increase in center time and choice-related behavior over the course of each trial. Regardless of the amount of information represented in memory at any given time, a greater amount of memory processing would be required late in the task, when a large number of arms need to be compared to the information in memory before a correct one is found. Earlier in the task, relatively fewer arms need to be explored before an unvisited arm is found. Thus, the changes in behavior found in the present experiments may reflect differences in the *use* of memory rather than differences in the amount of information represented in memory.

In addition to showing that the factors guiding choices in the radial maze change over the course of each trial, the present data indicate that the typical measure of errors does not capture the apparent fact that rats often choose arms despite a lowered expectation of finding food. This is shown by the difference in mean running time to correct vs. incorrect choices. That animals sometimes make errors despite an anticipation of nonreward has previously been shown by Wilkie and Spetch (1981). One explanation for such effects is that the memories guiding choice behavior are not all-or-none, but can exist in intermediate states (Roberts & Grant, 1976; Roitblat, 1980). Alternatively nonmemorial processes, such as "choosing impulsively" or "guessing," may be involved in choices on some trials (Wilkie & Spetch, 1981). If so, the use of such processes may increase running times as well as decrease accuracy. The distributions of running times, shown in Fig. 5, suggest that some errors are made when the rat has no information about previous visits to the arm (running time equivalent to correct choice), while other errors are made despite the presence of such information (longer running time).

The present experiment shows that more information can be gleaned from the behavior of rats in the radial maze than is available from simple measures of accuracy. The measures used in the present experiment suggest that complex changes in the behavior of rats and the processes underlying that behavior occur during the course of each trial. During the early part of the choice sequence, choices are made quickly and with a relatively great degree of response bias. After a number of choices have been made, the prevalence of response biases decreases. A corresponding increase in the time spent in the center arena between choices may reflect an increase in the use of memory. Furthermore, simple measures of accuracy do not reflect the information that rats have about the correctness of their choices. Thus, theories that treat all choices in the radial maze as the product of a single static process must be critically

examined. A more dynamic view will be required for any complete understanding of the choice behavior of rats in the radial maze.

REFERENCES

- Attneave, F. (1959). *Applications of information theory to psychology*. New York: Henry Holt.
- Beatty, W. W., & Shavalia, D. A. (1980). Spatial memory in rats: Time course of working memory and effect of anesthetics. *Behavioral and Neural Biology*, **28**, 454–462.
- Bond, A. B., Cook, R. G., & Lamb, M. R. (1981). Spatial memory and the performance of rats and pigeons in the radial-arm maze. *Animal Learning and Behavior*, **9**, 575–580.
- Capaldi, E. J., & Verry, D. R. (1981). Serial order anticipation learning in rats: Memory for multiple hedonic events and their order. *Animal Learning and Behavior*, **9**, 441–453.
- Cook, R. G., Brown, M. F., & Riley, D. A. (1985). Flexible memory processing by rats: Use of prospective and retrospective information in the radial maze. *Journal of Experimental Psychology: Animal Behavior Processes*, **11**, 453–469.
- DiMattia, B. V., & Kessner, R. P. (1984). Serial position curves in rats: Automatic versus effortful information processing. *Journal of Experimental Psychology: Animal Behavior Processes*, **10**, 557–563.
- Ellis, M. E., Clegg, D. K., & Kesner, R. P. (1984). Exhaustive memory scanning in *Rattus norvegicus*: Recognition for food items. *Journal of Comparative Psychology*, **98**, 194–200.
- Hulse, S. H. (1978). Cognitive structure and serial pattern learning by rats. In S. H. Hulse, H. Fowler, & W. K. Honig (Eds.), *Cognitive processes in animal behavior*. Hillsdale, NJ: Erlbaum.
- Jensen, G. D., & Rey, R. P. (1969). "Horn of plenty" conditions versus gradual diminution of reward supply with extended training. *Journal of Experimental Psychology*, **80**, 190–191.
- Kesner, R. P., & Novak, J. (1982). Serial position curve in rats: Role of the dorsal hippocampus. *Science*, **218**, 173–174.
- Kissileff, H. R. (1969). Food-associated drinking. *Journal of Comparative and Physiological Psychology*, **67**, 284–300.
- Mazmanian, D. S., & Roberts, W. A. (1983). Spatial memory in rats under restricted viewing conditions. *Learning and Motivation*, **14**, 123–139.
- Olton, D. S. (1978). Characteristics of spatial memory. In S. H. Hulse, H. Fowler, & W. K. Honig (Eds.), *Cognitive processes in animal behavior*. Hillsdale, NJ: Erlbaum.
- Olton, D. S., Becker, J. T., & Handlemann, G. E. (1979). Hippocampus, space and memory. *The Behavioral and Brain Sciences*, **2**, 313–365.
- Olton, D. S., & Collison, C. (1979). Intramaze cues and "odor trails" fail to direct choice behavior on an elevated maze. *Animal Learning and Behavior*, **7**, 221–223.
- Olton, D. S., & Samuelson, R. J. (1976). Remembrance of places passed: Spatial memory in rats. *Journal of Experimental Psychology: Animal Behavior Processes*, **2**, 97–116.
- Roberts, W. A. (1979). Spatial memory in the rat on the hierarchical maze. *Learning and Motivation*, **10**, 117–140.
- Roberts, W. A. (1981). Retroactive inhibition in rat spatial memory. *Animal Learning and Behavior*, **9**, 566–574.
- Roberts, W. A., & Dale, R. H. I. (1981). Remembrance of places lasts: Proactive inhibition and patterns of choice in rat spatial memory. *Learning and Motivation*, **12**, 261–281.
- Roberts, W. A., & Grant, D. S. (1976). Studies of short-term memory in the pigeon using the delayed matching-to-sample procedure. In D. L. Medin, W. A. Roberts, & R. T. Davis (Eds.), *Processes of animal memory*. Hillsdale, NJ: Erlbaum.

- Roberts, W. A., & Smythe, W. E. (1979). Memory for lists of spatial events in the rat. *Learning and Motivation*, **10**, 313-336.
- Roitblat, H. R. (1980). Codes and coding processes in pigeon short-term memory. *Animal Learning and Behavior*, **8**, 341-351.
- Sternberg, S. (1969). Memory-scanning: Mental processes revealed by reaction-time experiments. *American Scientist*, **57**, 421-457.
- Suzuki, S., Augerinos, G., & Black, A. H. (1980). Stimulus control of spatial behavior on the eight-arm maze in rats. *Learning and Motivation*, **11**, 1-18.
- Walker, J. A., & Olton, D. S. (1979). The role of response and reward in spatial memory. *Learning and Motivation*, **10**, 73-84.
- Wilkie, D. M., & Spetch, M. L. (1980). Pigeons' delayed matching to sample errors are not always due to forgetting. *Behaviour Analysis Letters*, **1**, 317-323.
- Yoerg, S. I., & Kamil, A. C. (1982). Response strategies in the radial arm maze: Running around in circles. *Animal Learning and Behaviour*, **10**, 530-534.

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