

In the dark: Spatial choice when access to spatial cues is restricted

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The cognitive mechanisms involved in spatial choice when access to visual cues is restricted were examined in three experiments using male rats. A specially constructed radial-arm maze was used, in which extramaze visual cues could not be perceived from the central arena, but could be perceived from the maze arms. Choices were very accurate when the maze was not rotated during each trial, but inaccurate when the maze was rotated. This suggests that intramaze cues were involved in the control of choices. However, the data clearly showed that choices were not simply controlled by intramaze cues. Rather, control by intramaze cues interacted in a more complex manner with representations of the spatial locations of goals. Such spatial representations were involved in the control of choice despite the absence of visual spatial cues at the time choices were made.

Behavioral and neurophysiological evidence has recently been used to argue that spatial choices and spatial discriminations are controlled by specialized mechanisms (see, e.g., Cheng, 1986, 1988; Etienne, Lambert, Reverdin, & Teroni, 1993; Gallistel, 1990; Leonard & McNaughton, 1990; McNaughton, Chen, & Markus, 1991; O'Keefe, 1991; O'Keefe & Nadel, 1979; Poucet, 1993). The radial-arm maze (RAM) paradigm has provided some of the critical data falling into this category.

Ironically, Brown (1992) has shown that performance in the standard RAM can be explained without recourse to any specialized mechanisms of choice. Brown developed a sequential choice model of RAM performance, according to which go/no-go decisions are made about individual maze arms. Rats observe the extramaze cues corresponding to a maze arm and either visit the arm or reject it. If the arm is rejected, the cues corresponding to another arm are observed and another decision is made. Each of these instances of cue observation and decision (termed a *microchoice*) is independent of previous microchoices. Furthermore, the identity of the arm serving as the target of a microchoice is not influenced by the location of baited arms (i.e., correct maze arms are no more likely to serve as the target of microchoices than would be expected by chance). Thus, each arm visit (a *macrochoice*) is preceded by one or more microchoices, and a microchoice is the behavioral expression of each choice.

Support for this model came from analysis of the rat's behavior in the central arena of the maze. Rats typically hesitate at the threshold leading to maze arms and visually orient toward the end of the arm. This behavior oc-

curs more frequently toward the end of trials, when most arms have been depleted of food (Brown, 1993, Figures 9.2 and 9.3; Brown & Cook, 1986). Brown (1992) assumed that each instance of this behavior represents a microchoice. Given this assumption, microchoice outcomes provide a very accurate prediction of macrochoice accuracy, as well as of the number of microchoices that make up each macrochoice (termed *choice efficiency*). Thus, the sequential choice model provides an accurate description of performance in the standard RAM. It is important to emphasize that the sequential choice model requires no specialized spatial abilities. Rats are hypothesized to choose maze arms simply on the basis of the visual cues corresponding to the arms. They have no special ability allowing them to "locate" arms or navigate toward them.

However, Brown, Rish, VonCulin, and Edberg (1993) have recently shown that the sequential choice model fails under a set of identifiable conditions. Specifically, when access to visual extramaze cues from the central arena is restricted and requires an effortful observing response, rats' behavior is *spatially guided* to baited arms. The most direct evidence for this conclusion came from an experiment in which behavior in a RAM in which rats had to push open hinged doors in order to gain access to maze arms (to make a microchoice and/or visit the arm) was compared with behavior in the same maze without these doors. When the doors were present, the target of a microchoice was more likely to be a correct (baited) arm than would be expected by chance. When the doors were not present, the target of a microchoice was no more likely to be a correct arm than would be expected by chance (as was the case in the experiments of Brown, 1992). In essence, when there was easy access to extramaze cues, choice behavior was not controlled by the location of baited arms until the visual cues corresponding to those locations were available. When access was restricted, on the other hand, rats were spatially guided toward the location of a correct (baited) arm.

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These results suggest that there are two different modes of spatial performance in the RAM. The first predominates in the standard (open) RAMs used in the vast majority of previous experiments. Under these conditions, rats are simply accepting or rejecting visual stimuli, namely the stimuli corresponding to the view of the arm from the central arena. The second mode occurs when access to the visual extramaze stimuli is restricted. Under these conditions, rats somehow perceive their current location in space, represent the locations of goals, and are thereby guided to those locations.

These two hypothetical modes of spatial choice correspond closely to two sets of processes described by Gallistel (1990). Gallistel has argued that spatial performance is sometimes controlled by specific stimuli, located in proximity to the target location, which animals simply move toward or away from (termed *beacon homing*). This corresponds to rats in the RAM accepting or rejecting individual maze arms on the basis of the stimuli corresponding to each arm, as according to the sequential choice model of Brown (1992, 1993). Gallistel has argued that animals also use a *cognitive map* in combination with *dead reckoning* during spatial performance. Dead reckoning allows the animal to determine its current location, relative to a starting point or relative to a mapped representation of multiple points, by continuously monitoring its direction and velocity of movement. Dead reckoning, in combination with a cognitive map, provides a possible mechanism for spatial guidance in the RAM when access to extramaze cues is restricted. It is possible that choice behavior is controlled by visual stimuli corresponding to each arm (beacon homing, in Gallistel's terms) when there is unrestricted access to extramaze visual cues, but choice behavior is controlled by processes specialized for spatial performance (e.g., dead reckoning and cognitive mapping) when access is restricted.

Gallistel's (1990) views provide one particular set of hypotheses that correspond to our more general claim that spatial choices can be controlled either by very common choice processes (e.g., beacon homing as a form of simple stimulus approach) or by processes that are specialized for spatial choice. If Brown et al.'s (1993) proposal that atypical conditions are necessary to elicit the use of specialized mechanisms for spatial guidance is correct, a new look at some basic phenomena in the RAM is required. This is because the vast majority of previous RAM studies have been conducted in standard mazes with unrestricted access to extramaze cues. But mechanisms specialized for spatial processing may not be involved in RAM performance unless such access is restricted. In the present series of experiments, performance in a specially constructed maze, designed to elicit spatial guidance by restricting access to extramaze cues, was examined. During the course of these experiments (Experiment 2), it became clear that procedures which do not disrupt choice accuracy in the standard RAM are very disruptive in this specialized maze. Experiment 3 was designed to explain why, and to use this phenomenon to shed light on the mechanisms of spatial guidance.

EXPERIMENT 1

In the first experiment, performance in an RAM explicitly designed to eliminate access to extramaze cues from the central arena of the maze was examined. The central arena was completely enclosed so that subjects could not gain access to extramaze visual cues without opening a door or visiting an arm. Thus, although extramaze visual cues were available after subjects had made a choice and were on a maze arm, during the time that subjects were moving toward arms and choosing among arms, the stimuli (beacons) that are believed to control choice in the standard radial maze were not available.

In addition, relative to our earlier studies examining microchoices in the RAM, this maze rendered microchoices more effortful (because of the heavier doors which needed to be pushed open to gain access to extramaze visual cues) and arm visits less effortful, once a microchoice had been made (because of the short maze arms). We expected these changes in the relative effort required for microchoices and arm visits to reduce the number of arm rejections. As discussed below, this allowed us to directly measure spatial guidance in these experiments.

Method

Subjects. The subjects were 16 experimentally naive male Sprague-Dawley rats, approximately 4 months of age at the beginning of the experiment. They were maintained at 80% to 85% of free-feeding weight by supplemental feeding following each experimental session. Subjects were housed in groups of 3 or 4 and transported in their home cages between the colony and experimental rooms daily. Experimental sessions were conducted during the dark phase of a 12:12-h light:dark cycle.

Apparatus. The apparatus was the 12-arm radial maze shown in Figure 1. Its surface was constructed of 2.0-cm-thick plywood. The central arena was 60 cm in diameter. The central arena was surrounded by a 12-sided box, constructed of the same material and 30.5 cm tall. A hole in each wall of this box (7.5 cm in diameter and centered 4.7 cm above the maze surface) allowed entrance onto each maze arm. A lid, constructed of the same material as the box, was hinged to the box. Thus, the central arena was completely enclosed when this lid was closed. The 12 maze arms were 10 cm wide and 40 cm in length, and extended from the central platform at equal angles. A small container (2.0 cm square and 1.5 cm deep, open at the top) was attached to the end of each arm and served as the food cup. An enclosure (with walls and ceiling) was attached to each arm. These enclosures were constructed of thin (0.5-cm-thick) plywood and extended 26 cm from the central arena at a height of 15 cm. Metal doors in sliding tracks were located at the boundary between the box surrounding the central arena and each of these enclosures. These doors were used to control access to each arm by way of a string-and-pulley system. An additional set of doors was located at the end of each enclosure facing the end of the maze arm. These doors were constructed of 2.0-cm-thick plywood. They were hinged at the top of the enclosure so that a rat could push them open to allow exposure to extramaze cues or to gain access to the food cup. The food cups were close enough to these doors that the doors were held open by the rat's body as it visited the food cup, allowing the rat to return to the central arena. A microswitch located inside each enclosure allowed any movement of these wooden doors to be detected electronically. The maze was elevated 62 cm above the floor of the room. A lazy Susan was used to mount the maze onto a small table: This allowed the maze to be easily rotated relative to extramaze cues. The maze was painted flat black, inside and outside.

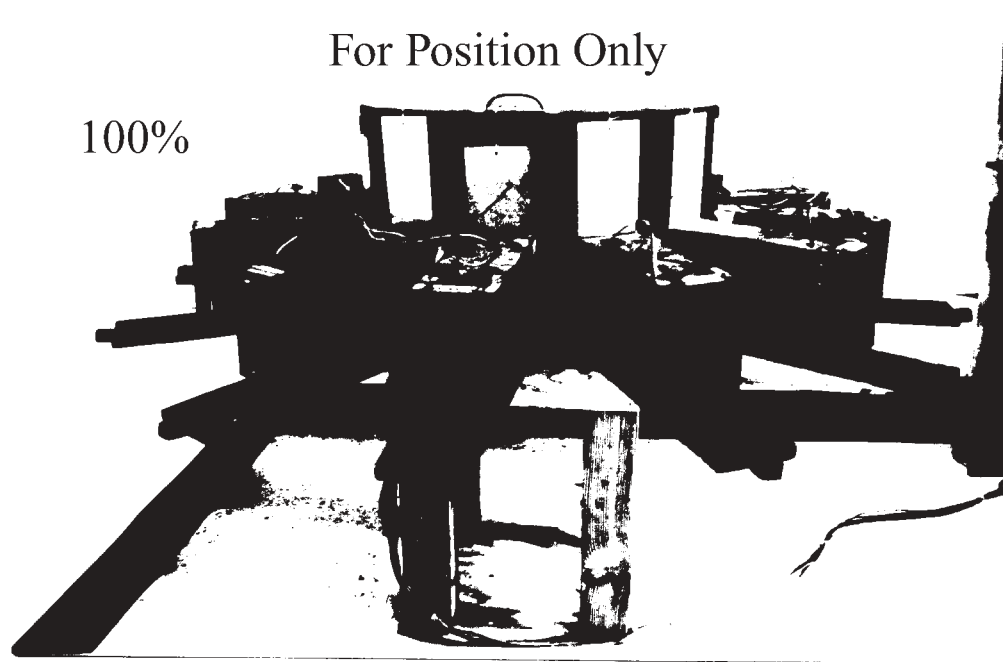


Figure 1. Photograph of the apparatus. The central arena and part of each maze arm are enclosed. A metal guillotine door at the junction between the central arena and the enclosed portion of each arm can be used to control access to individual maze arms. A wooden door, hinged at the top, must be pushed open in most experimental conditions to allow visual or ambulatory access to the maze arm.

The experiment was conducted in a 4.4×3.6 m room, illuminated by fluorescent tubes and rich in extramaze visual cues.

Training. Rats were first given the pellets to be used in the experiment (BioServe 45-mg sucrose pellets) in their home cage for 3 consecutive days. They were then shaped to visit maze arms and eat food from the food cups in a series of daily trials. The metal doors were not present during training, and the hinged wooden doors were fully opened (they were hinged so that they could rest in the open position on top of the enclosures). The lid on the central arena was also propped open. During the earliest training sessions, pellets were scattered in the central arena and on the arms of the maze. Two pellets were placed in each food cup. Rats were placed in the maze in groups of 3 or 4 (cage mates). They were allowed to consume pellets and visit maze arms until all pellets were consumed or approximately 15 min elapsed.

Once a rat consistently visited arms and ate pellets from the food cups, it received daily individual sessions. Prior to each session, each maze arm was baited with two pellets, the rat was placed in the central arena, and the lid was closed. A procedure was used to shape rats to push open the hinged wooden doors in order to enter maze arms. A set of strings and/or shims (placed where the door was hinged to the enclosure) were used to hold the wooden doors open at different heights. During initial sessions, the doors were held open at a height allowing the rat to enter arms unimpaired. If a rat completed the maze (visited all 12 arms), the door was lowered slightly for the next daily session. Using this method of successive approximations, each rat was trained to push open doors from the fully closed position. This training procedure required approximately 25 trials (range for rats that completed training = 20–32).

Testing. Prior to each trial, each food cup was baited with two sucrose pellets. The metal doors were removed from their tracks (they were not used in Experiment 1). The wooden doors were closed. The maze was rotated into one of four equally spaced orientations, randomly chosen. The lid of the central arena was opened

just long enough to place the rat in the center of the maze. The rat was then allowed to visit arms until all 12 arms had been visited, 24 choices had been made, or 10 min had elapsed. Any movement of the wooden door was detected electronically using the microswitches. Any door movement was considered to be a microchoice (Brown, 1992; Brown et al., 1993). Arm visits (macrochoices) were defined as the rat's snout crossing the plane defined by the end of the maze arm (the food cup being located just beyond this plane). A case in which a microchoice occurred, but the rat did not continue to visit the arm, was considered to be an arm rejection. For each rat, 1 trial per day was conducted for a total of 20 trials.

Results

Four rats failed to complete the training phase of the experiment. It appeared that this failure was a function of the requirement that the wooden doors be pushed open to gain access to the maze arms.

The primary result of this experiment was that choices were very accurate. During the 20 test sessions, completion of the maze required a mean (over rats) of 13.3 choices. This value is clearly different from that expected on the basis of chance. For example, a Monte Carlo estimate of chance was conducted in which 12 alternatives were sampled until all 12 had been selected. To mimic the fact that rats almost never immediately return to the just-chosen arm, the program never selected the same alternative twice in succession. Aside from this restriction, the alternatives were chosen randomly. One thousand iterations of this algorithm produced an estimate of chance of 33.6 choices to complete the maze. This value is significantly larger than the obtained value [$t(11) =$

68.8] ($p < .05$ was the criterion used for this and all statistical decisions reported in this paper). On the other hand, the obtained value is very close to perfect performance (i.e., 12.0 choices to complete the maze).

A critical ancillary result of the experiment was that there were very few arm rejections. That is, rats very seldom pushed open a hinged wooden door (a microchoice) without continuing through the door to visit the arm (a macrochoice). The mean (over rats) number of arm rejections per trial was 0.41 (range = 0.0–0.8).

In addition, it did not appear that the rats moved from arm to arm in a stereotypical fashion. The modal spatial separations between one arm and the one chosen next were 1, 2, and 3 arm distances for 3, 3, and 6 rats, respectively. The proportion of arm separations that had the modal value ranged (over rats) from .27 to .75 ($M = .42$).

Discussion

In this experiment, rats chose maze arms without the benefit of access to extramaze visual cues. While the rat was in the central arena of the maze (or in the enclosure on a maze arm), it was not exposed to the extramaze visual stimuli that clearly control spatial choice in the standard radial maze (e.g., Brown, 1992; Mazmanian & Roberts, 1983; Suzuki, Augerinos, & Black, 1980; Zoladek & Roberts, 1978). Because rats virtually never acquired extramaze visual information without visiting the arm (i.e., arm rejections were very rare), choices of maze arms were made in the absence of extramaze visual information. Once the rat made a choice (and thus visited a maze arm), it was exposed to extramaze visual cues. But because each choice was made prior to opening the hinged door, choices could not have been controlled by perceived extramaze cues. Despite this apparent handicap, rats chose maze arms in this experiment as accurately as rats have in any experiment using a 12-arm maze. This result replicates the results of Brown et al. (1993), who also found high levels of choice accuracy when access to extramaze visual cues from the central arena of a radial maze was restricted.

The lack of arm rejections is in contrast to the results of our earlier experiments in which microchoices were measured (Brown, 1992; Brown & Huggins, 1993; Brown & Lesniak-Karpiak, 1993; Brown et al., 1993). In our earlier experiments, in which a maze with restricted access to extramaze visual cues was used (Brown et al., 1993), rats typically observed several maze arms before visiting one (at least toward the end of the choice sequence). The present maze was designed to discourage these arm rejections. The hinged doors in the present experiment required more effort to push open (their mass was 155 g in contrast to the 45-g hinged doors used by Brown et al., 1993, Experiments 2–5). The maze arms were approximately half the length of the standard-length arms used in our earlier experiments. In combination, these design features of the apparatus were intended to decrease the difference in effort required for a microchoice followed by an arm rejection and a microchoice

followed by an arm visit, thereby decreasing the tendency of the rats to reject maze arms. This expectation was based on previous research from our laboratory indicating that effort affects a choice criterion in the radial maze (Brown & Huggins, 1993; Brown & Lesniak-Karpiak, 1993).

The fact that rats did not observe visual cues prior to making choices allowed standard measures of choice accuracy in the radial maze to reflect the guidance of spatial choices without having to filter out the effects of a sequential choice process (Brown, 1992, 1993; Brown et al., 1993). In fact, we had originally planned to apply the sequential choice model to the present data in order to determine the extent to which choices were spatially guided. The virtual lack of arm rejections made this both impossible and unnecessary. Because rats in the present experiment only looked at cues corresponding to arms that they also visited, the high levels of choice accuracy obtained in this experiment must have been supported by something other than perceived visual cues.

EXPERIMENT 2

There is abundant evidence that visual extramaze cues are critical for performance in the standard radial maze. The results of Brown et al. (1993, especially Experiment 3) suggest that the processes underlying radial maze performance may differ when access to extramaze visual cues from the central arena is restricted. The results of Experiment 1 indicate that whatever these alternate processes are, they can support very accurate spatial performance. Our intention was to examine the processes that produce the accurate performance obtained in this maze.

To do this, we planned to perform various manipulations during the course of each trial. With this goal in mind, we first developed a forced-choice procedure for the maze used in Experiment 1, designed to be analogous to forced-choice procedures used in our and many others' RAM experiments (e.g., Brown, 1992). We expected the rats to perform accurately in this procedure, as they have in forced-choice procedures used in earlier experiments, including our experiments in which access to visual cues was restricted (Brown et al., 1993).

Method

Subjects and Apparatus. The subjects were the 12 rats that had completed Experiment 1. The apparatus was the same as that used in Experiment 1.

Procedure. The experiment began immediately following the completion of Experiment 1. Prior to each trial, each food cup was baited with two pellets. The maze was rotated into one of the four randomly chosen orientations. All 12 metal doors were closed and all 12 wooden doors were opened. The rat was placed in the central arena by lifting the lid on the arena, placing the rat in the center, and closing the lid. Approximately 5 sec later, the metal door leading to one (randomly selected) maze arm was lifted remotely using the string-and-pulley system. The rat was allowed to visit this arm. As it did so, the door to a second (randomly chosen) arm was opened. Subsequently, as the rat visited each scheduled arm, the door to the previous arm was closed and the door to the next arm was opened. This process continued until the rat had visited a sequence of six

different maze arms. When the rat returned to the central arena following the sixth arm visit, the lid was opened and the rat was removed and placed in a small holding cage, distinct from the home cage. The rat remained in this delay interval for 15 min, during which time other rats were placed in the maze for their experimental sessions.

Upon the return of the rat to the maze, the orientation of the maze had been randomly chosen from among the four possibilities, with the restriction that it not be the same as the orientation during the first portion of the trial. The six arm locations that had been visited during the forced-choice phase were not baited, and the remaining six were baited (it should be emphasized that maze arms were baited according to their location in space). The metal doors were removed and the wooden doors were closed. Thus, the rat was free to choose from among the maze arms, but had no access to visual cues in the central arena and had to push open the hinged wooden doors in order to gain access to the visual cues or the food cups. The lid was opened, the rat was placed in the central arena, and the lid was closed. The sequence of microchoices was recorded electronically and the sequence of macrochoices (arm visits) was recorded by the experimenter. Arm visits were identified according to the location of the maze arm. A trial was terminated when the rat had visited the six baited locations or 10 min had elapsed since the return to the maze. The experiment was conducted until a rat had completed 20 daily trials.

Results

Three rats failed to complete the experiment. It appeared that their behavior was disrupted by the forced-choice procedure, in that they failed to visit arms when the metal doors were being used to obstruct access to other maze arms.

Among the remaining 9 rats, a mean of 16.9 choices was required to complete the maze (this includes the six forced choices made prior to the delay). The source of the choice errors was almost exclusively the arms that had been visited prior to the delay. Specifically, the mean number of errors to arms that had been visited during the forced-choice phase of the trial was 4.7. The mean number of errors to arms that were initially visited following the delay was 0.2. To allow a comparison of the former value to an estimate of chance, a Monte Carlo simulation was developed in which six maze arms were first randomly chosen without replacement (to mimic the forced-choice trial segment). The simulation then chose randomly from among the 12 arms (mimicking the free-choice segment), with the restriction that arms visited during the free-choice segment never be revisited (just as they virtually never were in the empirical results). The mean (over 1,000 simulation runs) number of arms chosen during the forced-choice segment that were then revisited during the free-choice segment was 5.1, which is not significantly different from the mean empirical value of 4.7 [$t(8) = 1.1$].

As in Experiment 1, very few arm rejections occurred. The mean (over rats) number of microchoices per trial that were not accompanied by an arm visit was 0.2.

An analysis was developed to determine if choices during the free-choice segment of each trial were being controlled by intramaze cues, such as an odor mark left on arms or distinctive cues in the maze itself. The analysis was restricted to the first five trials of the experiment

in order to allow for the possibility that the use of intramaze cues was in operation during Experiment 1 (when it would have allowed the rat to complete the maze accurately), but extinguished during Experiment 2 (because it was not supported by the contingencies in operation, i.e., the baiting of maze arms according to location). The analysis was designed to allow control of arm visits by their location in space to be dissociated from control of arm visits by their physical identity.

The first six arm visits during the free-choice segment of each of these trials were analyzed. Maze arms were classified according to two properties. First, the physical maze arm itself (independent of its location) either was or was not visited during the forced choices. Second, the spatial location of the maze arm (independent of the status of the arm in it) either was or was not visited during the forced choices. The probability of visiting maze arms (during the first six free choices) of each of four types defined by these two properties was determined for each rat. Figure 2 shows the means of these probabilities. Because there were 12 maze arms and the probabilities are calculated over six choices, the probability expected by chance is approximately .5. A repeated measures analysis of variance (ANOVA) was performed comparing the mean probabilities of visiting maze arms as a function of whether the maze arm itself and its location had been visited during the forced choices. There was no evidence that these probabilities differed as a function of the visited status of the maze arm [$F(1,8) < 1$] or the visited status of the location [$F(1,8) < 1$], nor that the effects of these variables interact [$F(1,8) = 0$].

Discussion

These results are quite different from those of Experiment 1 and those of previous experiments using seemingly similar procedures. The best way to summarize the basic result is that the pre-delay (forced) choices had no

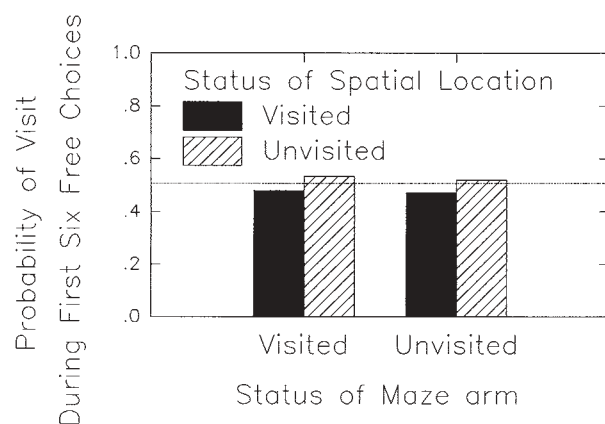


Figure 2. Data from the rotation analysis of Experiment 2. Shown are the mean probabilities of visiting maze arms during the first six free choices following trial interruption, as a function of whether the maze arm and location were visited during the forced choices. Random choice would result in approximately .5 of the arms of each type being visited.

effect on post-delay choice behavior. In essence, the rats behaved as though the beginning of the free-choice segment of each trial was a new trial. Thus, in contrast to the results of a large number of previous experiments from this and other laboratories, a 15-min delay produced a large disruptive effect in the present experiment. This finding is also in contrast to the results of Brown et al. (1993), who also used a maze with restricted access to extramaze cues but obtained high levels of choice accuracy following a forced-choice procedure and a 15-min delay.

One possible explanation for the disruption of choice accuracy in this experiment is the rotation of the maze during the delay. There is abundant evidence that maze rotation, and the intramaze cues it is designed to disrupt, have little or no effect in the standard RAM (see, e.g., Olton & Collison, 1979). But because the apparatus used in the present experiments was explicitly designed to prevent the use of perceived extramaze cues while the rat was in the central arena, it is reasonable that intramaze cues might be used under these atypical conditions. However, the analysis of the errors made during the first five trials of the present experiment provides no evidence that the choices during the free-choice segment of each trial were controlled by the physical identity of the maze arm. This is in agreement with the conclusions of Brown et al. (1993, Experiments 2 and 5), who found no evidence for the use of intramaze cues under conditions that were similar to the present ones.

EXPERIMENT 3

Experiment 3 was intended to explore some of the factors that might have contributed to the disruption of choice accuracy in Experiment 2. Prior to Experiment 3, the rats used in the experiments reported above were exposed to a sequence of pilot experiments examining various factors that might explain the difference between performance in Experiments 1 and 2. These pilot experiments involved a range of deviations from the free-choice and forced-choice procedures used in Experiments 1 and 2, respectively. The conditions were formulated to permit examination of the roles of the effort required to push open the wooden doors and the manipulation and handling of the subject during the forced-choice procedure. Although the data from these pilot experiments will not be reported, they led us to believe that, despite the results of Experiment 2, intramaze cues might somehow be involved in performance in the enclosed RAM. This suspicion was based on the consistent finding that rotation of the maze reduced choice accuracy.

Of course, the results of the rotation analysis of Experiment 2 show clearly that rats were not simply controlled by intramaze cues associated with individual maze arms. However, it remains possible that intramaze cues are involved in performance in a more subtle (and theoretically interesting) fashion. Specifically, intramaze cues could be incorporated into a cognitive map that also includes extramaze cues. As Brown et al. (1993) pointed out, there

is no fundamental distinction between extramaze and intramaze cues from the rat's point of view. If both kinds of cues are incorporated into a representation of space, and the maze is rotated, the ability of the rat to use its representation of space will be disrupted. But this does not necessarily imply that choices will be controlled by intramaze cues, which is what was measured by the rotation analysis used in Experiment 2. Rats may not be simply controlled by extramaze cues *or* intramaze cues, but rather by an amalgamation of both. If so, rotation of the maze would be expected to disrupt choice accuracy, but choices would not be expected to simply "follow" the intramaze cues to the locations into which they are rotated. Thus, it remains possible that rotation of the maze is the critical factor determining choice accuracy levels in the present experiments.

A second explanation for the disruption of choice accuracy in Experiment 2 focuses on the movement of the rat during the delay and the possible involvement of dead reckoning (Etienne, Sitbon, Dahn-Hurni, & Maurer, 1994; Gallistel, 1990) in rats' ability to perform in the enclosed RAM. Subjects' reckoned position or perceived orientation (*heading*, Margules & Gallistel, 1988) in the central arena may be disrupted by the movement that occurs while the rat is removed from the maze and spends time in the delay cage, thereby reducing choice accuracy.

The present experiment tested these two possibilities using two experimental manipulations. First, during some trials, the maze was rotated following six forced choices, whereas during others it was not rotated. Second, during some trials, the rat was removed from the maze during a short delay, whereas during others it remained in the central arena during the delay. The latter manipulation was motivated by the possibility that the rat's heading, relative to maze arms, would be harder to maintain when the rat is removed from the maze than when it remains in the maze.

Method

Subjects and Apparatus. The subjects were the 7 rats that completed the pilot experiments immediately preceding this experiment. The pilot experiments had required 18 daily trials in the enclosed RAM. The apparatus used in the present experiment was the same as that used in the previous experiments.

Procedure. During each trial, the rats were first given six forced choices. The procedure for conferring these forced choices was the same as that used in Experiment 2, except that the maze was in the same standard orientation (relative to extramaze cues) during the forced choices of every trial for every subject.

When the rat returned to the central arena following the sixth forced choice, a timer was started to measure a 3-min delay interval. During this delay, rats were exposed to one of four experimental conditions. In the "remove" conditions, the rat was removed from the maze and placed in a cage identical to those used for the same purpose in Experiment 2. In the "center" conditions, the rat remained in the center during the delay without the lid being lifted. In the "rotate" conditions, the maze was rotated to one of four positions (either one or two arm distances clockwise or counterclockwise, relative to the standard orientation). In the "nonrotate" conditions, the maze was not moved from the standard position. These experimental conditions were combined factorially to form four ex-

perimental conditions (center/rotate, center/nonrotate, remove/rotate, and remove/nonrotate). Note that in the center/rotate condition, the maze was rotated with the rat in the central arena.

Following the delay, the rat was returned to the maze (if necessary) and allowed to choose from among all 12 maze arms. The metal doors were open during this portion of each trial. The spatial locations that had been visited prior to the delay did not contain pellets, whereas the locations that had not been visited were baited. Rats were allowed to make choices until all 12 spatial locations had been visited (including pre-delay visits).

The four experimental conditions were manipulated within subjects, in four randomized blocks of four daily trials each.

Results

One rat failed to complete the experiment. It ceased making choices following the delay during the first block of trials. Its data are not included in the analyses. The other 6 rats completed all 16 trials, with the exception of 1 rat that failed to complete one trial (5 min elapsed without a choice). Data from that one trial were not included in the analysis.

Figure 3 shows the mean number of choices required to complete the maze in the four conditions of the experiment. An ANOVA revealed that more choices were required when the maze was rotated than when it was not [$F(1,5) = 40.0$]. However, there was no difference in choices required when the rat was removed from the maze as opposed to when it remained in the central arena [$F(1,5) = 3.1$]. Nor was there evidence that the effects of these variables interacted [$F(1,5) = 1.5$].

In order to understand the effect of maze rotation, the analysis developed in the context of Experiment 2 was applied to the data from the center/rotate and remove/rotate conditions. The probability of visiting an arm during the first six choices following the trial interruption

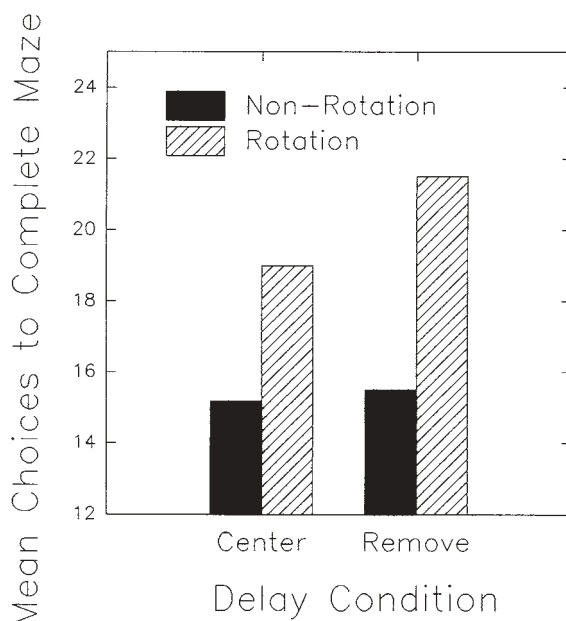


Figure 3. The mean number of choices required to complete the maze in the four experimental conditions of Experiment 3.

was determined as a function of whether the maze arm and location had been visited during the forced choices. Figure 4 shows the means of these probabilities for the two conditions of experiment in which the maze was rotated. A 2 (experimental condition) \times 2 (visited status of the maze arm) \times 2 (visited status of the spatial location) repeated-measures ANOVA was performed. Maze arms visited during the forced choices were less likely to be visited than those not visited [$F(1,5) = 17.7$]. Locations visited during the forced choices were also less likely to be visited than those not visited [$F(1,5) = 15.6$]. There was no evidence of an interaction between the effects of these variables [$F(1,5) = 3.8$], nor was there evidence for any interactions involving experimental condition.

Discussion

Comparison of choice accuracy in the remove and center conditions provides no evidence that rats' choice accuracy was disrupted by removal from the maze. Of course, this null result must be interpreted with caution. It remains possible that part of the disruptive effects of the manipulations used in Experiment 2 was due to the greater amount of movement outside the maze that occurred during the longer delays used in that experiment.

However, the present results do clearly indicate that rotation of the maze disrupts performance in the enclosed RAM. This effect implies that intramaze cues control choices in this maze. The results of the rotation analysis confirm this conclusion. However, the results of the rotation analysis make it equally clear that choices are also controlled by the spatial location of maze arms. Furthermore, because the visual cues corresponding to those spatial locations are absent at the time the choices are made, control by spatial location must rely on a representation of locations that can be used in the absence of those cues. Thus, we conclude that intramaze cues and a representation of spatial locations jointly controlled choices in the present experiment.

This conclusion regarding the role of intramaze cues is in agreement with the results of Brown et al. (1993, Experiment 5). On the basis of different experimental logic, Brown et al. also concluded that, at least under conditions of restricted access to extramaze cues, extra- and intramaze cues are mapped together on a cognitive map and that disruption of the integrity of that representation results from rotation of the maze. Aside from the practical implication that maze rotation is not a simple experimental manipulation under these conditions, this conclusion suggests that a wide range of spatial cues can be involved in RAM performance.

GENERAL DISCUSSION

The results of these experiments include several novel findings that, on the basis of the earlier findings of Brown et al. (1993), we assume resulted from the restriction of access to extramaze visual cues. Perhaps the two most important of these appear superficially to be mutually incompatible, but they are not. First, rats performed very accu-

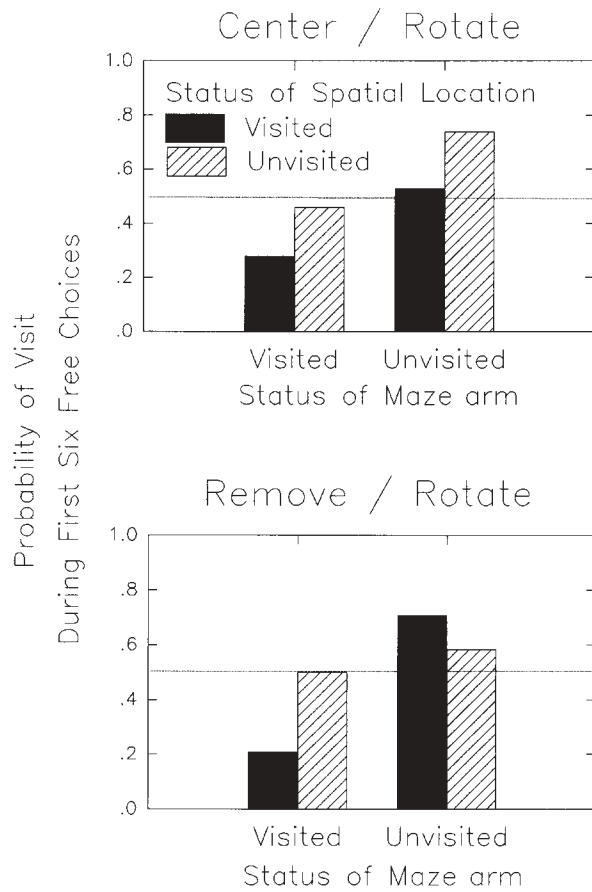


Figure 4. Data from the rotation analysis of the center/rotate and remove/rotate conditions of Experiment 3. Shown are the mean probabilities of visiting maze arms during the first six free choices following trial interruption, as a function of whether the maze arm and location were visited during the forced choices. Random choice would result in approximately .5 of the arms of each type being visited.

rately in an enclosed RAM if it was not rotated during a delay, but their ability to avoid revisits was severely reduced when the maze was rotated. Second, intramaze cues either had no direct control over choice (Experiment 2) or shared control with spatial location (Experiment 3). The first finding could be easily explained if rats simply used cues that rotate with the maze in discriminating previously visited and unvisited maze arms. These cues could be imperfections of the apparatus itself that distinguish maze arms or cues generated by the rats (e.g., an odor trail). However, the rotation analyses of the choices made during Experiments 2 and 3 clearly show that choices were not simply being controlled by intramaze cues.

The results of the rotation analysis of Experiment 3 indicate joint control of choices by intra- and extramaze cues. One version of how this joint control occurs is that a cognitive map is formed that combines intra- and extramaze cues. The integrity of such a map would be disrupted severely by maze rotation. Unfortunately, this view

of intra- and extramaze cue control cannot accommodate the procedural details of the experiments. Specifically, the orientation of the maze varied from trial to trial during the early experience of these rats in the enclosed RAM. (In fact, this was the case throughout these experiments, with the exception of the prerotation portion of each trial during Experiment 3.) Thus, intra- and extramaze cues were not located consistently relative to each other across trials. Therefore, no one cognitive map could incorporate cues of both types.

An alternative possibility is that two cognitive maps are formed, one consisting of extramaze cues and the other consisting of intramaze cues. These two maps could be aligned during the course of each trial to allow joint control by both cue types. As the rat visits arms and is thereby exposed to extramaze cues, the spatial relationship between the intramaze cues and extramaze cues

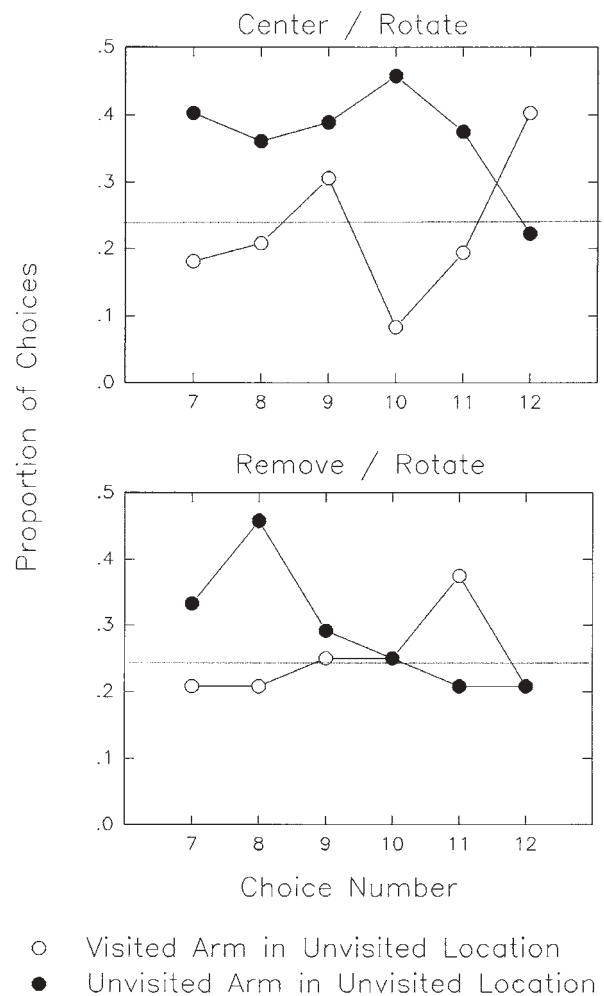


Figure 5. The proportion of choices made to locations not visited during the forced choices (containing either visited or unvisited maze arms) over the course of the first six postrotation choices. Data are from the two conditions of Experiment 3 in which the maze was rotated (top panel, center/rotate; bottom panel, remove/rotate). Random choice would result in approximately 25% of visits to each type of arm.

could be determined. This view predicts that control of choice by extramaze cues should increase as additional maze arms are visited. At the extreme, control by extramaze cues during the first postrotation choice should be impossible, because no information about the alignment of the maze relative to extramaze cues is available until after the first arm is chosen following rotation. Thus, the proportion of choices made to locations not visited prior to maze rotation should increase as the rat makes choices following maze rotation. Figure 5 shows these proportions, using the same data shown in Figure 4, but calculated over the course of the first six postrotation choices. There is no indication that the proportion of choices made to locations not visited prior to maze rotation increases over the course of choices. This fact argues against the idea that two separate maps are aligned as the rat is exposed to the position of extramaze cues relative to intramaze cues.

A final theory of how intra- and extramaze cues can jointly control choices in the enclosed RAM treats spatial cues internal to the rat (i.e., vestibular cues) as intramaze cues. There is some evidence that the vestibular system plays an important role in RAM performance (Ossenkopp & Hargreaves, 1993) and growing physiological evidence that spatial orientation (heading) is directly coded in several areas of the nervous system (e.g., Lavoie & Mizumori, 1994; McNaughton et al., 1991; Taube, Muller, & Ranck, 1990). These processes may in turn be involved in a dead reckoning system that allows animals to discriminate their position relative to a reference location (Gallistel, 1990). Dead reckoning could allow determination of the current location relative to a cognitive map of extramaze cues, even when those cues are not currently available. One can imagine that, in the present apparatus, rats might use such information to determine their position in the central arena and calibrate this determination using the extramaze cues available during arm visits. However, if dead reckoning or vestibular cues were responsible for performance in the present apparatus, maze rotation should have had little or no effect on performance, whereas location during maze rotation (in the rotating maze vs. removed from the maze) might be expected to have some effect. Neither of these predictions is consistent with the data. Thus, it does not appear that an understanding of the present data is to be found in dead reckoning or vestibular cues.

These considerations lead to the following conclusions: Rats somehow combine spatial information provided by intra- and extramaze cues even when the two sets of cues are not consistently aligned relative to each other. It is critical to note that this joint control occurs in the absence of the extramaze cues themselves. Thus, the spatial control by extramaze cues must involve a spatially organized representation of those cues (i.e., a cognitive map). At the same time, disruption of the spatial relations between intra- and extramaze cues by rotation of the maze strongly impairs spatial choice accuracy. The mechanism that produces this interaction between control of spatial choice by intra- and extramaze cues is not clear.

The rotation analysis indicates that there was no control of spatial choice following the delay by either extra- or intramaze cues in Experiment 2. In Experiment 3, on the other hand, there was evidence of joint control by both intramaze cues and by spatial location following the delay. There are at least three possible explanations for the discrepancy between the results of these two experiments. First, the additional experience in the maze acquired between the two experiments may have been important. For example, it may be that rats can use the relatively less salient intramaze cues, or determine their correspondence to the extramaze environment, only after a large number of trials in the maze. A second explanation is suggested by a difference in the procedures used in the two experiments. In Experiment 2, the orientation of the maze both before and after the delay varied unpredictably from trial to trial. In Experiment 3, on the other hand, the maze was oriented consistently during the pre-delay phase of each trial. Thus, there was a consistent correspondence between intra- and extramaze cues during the pre-delay (forced-choice) phase of each trial during Experiment 3. This may have encouraged the rats to use a combination of intra- and extramaze cues during Experiment 3 in a way that they could not during the earlier experiments. Unfortunately, both of these explanations are contradicted by the very accurate performance obtained in Experiment 1. Experiment 1 occurred earlier than the other experiments and involved inconsistent maze orientations from trial to trial. Complicating this issue even further is the fact that choice accuracy appeared to be the lowest during the experiment in which both intra- and extramaze cues controlled the initial choices following the delay (i.e., during Experiment 3). A third consideration regarding the discrepancy between the results of Experiments 2 and 3 allows a possible explanation for control by intramaze cues only in the latter experiment. Specifically, in the trials of Experiment 3, the delay that occurred following the forced choices was much shorter than the delay occurring during the trials of Experiment 2, and other rats were not placed in the maze during each rat's delay. These differences provide obvious explanations for a difference in control by odor trails in the two experiments, but it is less clear how they might explain the difference in control by spatial location.

Several previous experiments have indicated that restriction of extramaze cues produces atypical performance in the RAM, although the specific effects have varied. Mazmanian and Roberts (1983) used an unusual procedure in which rats were placed on maze arms, rather than choosing and ambulating onto the arms themselves. Mazmanian and Roberts then compared the tendency of the rats to avoid those arms as a function of the exposure time and extent of spatial view from the arm. The latter variable was manipulated by restricting the view from the end of the maze arm to varying degrees. Mazmanian and Roberts found that restricting the availability of extramaze cues had a large detrimental effect on choice accuracy. Foreman (1985) found that rats trained in a standard maze performed poorly when they were tested in

darkness. On the other hand, Jones Leonard, McNaughton, and Barnes (cited in McNaughton, 1989) found that rats could make accurate choices in darkness in the RAM as long as the lights were on at the beginning of each trial. McNaughton has interpreted these and other results in terms of the activation of a spatial representation by extramaze cues that can then be maintained in the absence of those cues (e.g., McNaughton, 1989; McNaughton et al., 1991).

Performance in the standard RAM can be understood in terms of a more general process of stimulus approach and avoidance without recourse to specialized spatial performance processes (Brown, 1992; Brown et al., 1993). When access to such visual stimuli is restricted, on the other hand, spatial choice appears to be under the control of a different set of processes. These processes include the guidance of rats toward baited locations without the benefit of visual stimuli corresponding to those locations (Brown et al., 1993). Brown et al. failed to find evidence for a contribution of intramaze cues to this spatial guidance, and therefore attributed it to a cognitive map of extramaze cues. The present results complicate this story. Intramaze cues do appear to be involved in performance in an enclosed RAM. However, they are involved in an as-yet-unidentified complex manner that includes the interaction of intramaze cues with represented extramaze cues.

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