Exposure to Spatial Cues Facilitates Visual Discrimination but Not Spatial Guidance

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The performance in a radial-arm maze of two groups of rats with restricted access to extra-maze visual cues was studied. One group received extensive exposure to the visual environment of the maze, whereas the second group was never exposed to the environment, aside from their experience in the maze itself. Spatial exposure resulted in a slightly improved ability to discriminate between previously visited and unvisited spatial locations, which can be explained on the basis of general perceptual learning processes. However, there was no evidence that spatial exposure resulted in control of choices by the spatial relations among the maze locations. These results are discussed in terms of theories of spatial learning which appeal to perceptual learning and cognitive mapping. © 1998 Academic Press

A dominant view of spatial ability is that organisms learn the spatial relations among places (e.g., O'Keefe & Nadel, 1979; Gallistel, 1990). This learning is typically described in terms of the formation of a cognitive map, the map being a representation (or set of representations) which codes information about the distance, direction, ordinal relations in space, and/or other spatial relations among objects and places in the environment. A large number of experiments, often using the radial-arm maze paradigm (Olton & Samuelson, 1976), have examined the existence and properties of such representations, as well as the physiological processes that underlie them (e.g., Brown, 1992; Brown, Rish, VonCulin, & Edberg, 1993; McNaughton, Chen, & Markus, 1991; O'Keefe, 1991; Poucet, 1993; Suzuki, Augerinos, & Black, 1980). Although there is little consensus about the details, most authors have concluded that at least some types of spatial relations are included in the representations used under at least some conditions by rats in the radial-arm maze.

Under some experimental conditions, rats in the radial-arm maze are spatially guided toward the location of baited arms, in the sense that they navigate toward the location of the arms prior to being exposed to the visual cues that correspond to them (Brown *et al.,* 1993; Schenk, Grobéty, &

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Gafner, 1997). Gallistel (1990) has described this type of spatial guidance as ''piloting,'' i.e., using knowledge of spatial relations between seen landmarks and unseen goals to locate the latter. Gallistel further argued that piloting requires a cognitive map which codes the spatial relations among locations. Thus, evidence for the spatial guidance of choices (piloting) in the radial-arm maze serves as one indication of the existence of a cognitive map.

Although it seems clear that spatial relations among locations and objects in the environment control behavior under at least some conditions, there is relatively little empirical information about the learning processes that produce this control. Recently, several detailed theoretical accounts of the acquisition of cognitive maps have been offered (Etienne, Maurer, & Séguinot, 1996; Gallistel & Cramer, 1996; McNaughton, Barnes, Gerrard, Gothard, Jung, Knierim, Kudrimoti, Qin, Skaggs, Suster, & Weaver, 1996; Poucet, 1993; Benhamou, Bovet, & Poucet, 1995). These theories include the idea that the nervous system combines representations of local views of the visual environment with knowledge of the relative locations of those local views to form a more global representation of the spatial relations among objects and places in the environment. Information about the relative location of local views is itself dependent on the animal being sensitive to its own position in an egocentric reference frame, which is accomplished using the process of path integration (Mittelstaedt & Mittelstaedt, 1982; also known as dead reckoning, Gallistel, 1990). Thus, by keeping track of its own motion, the animal determines the spatial relations among local views, thereby acquiring the information that forms the cognitive map.

The present experiment was intended to test this view of how cognitive maps are formed. As a starting point, the theory predicts that subjects must be exposed to the spatial relations among locations/objects in the environment in order for representations of those spatial relations to guide them toward the location of baited arms in the radial-arm maze. The present experiment examined this simple prediction by using a modified radial-arm maze in which only small perspectives of the visual extra-maze environment were available from inside the maze. Furthermore, these views corresponding to each maze location did not overlap (i.e., cues seen from one maze arm could not be seen from other maze arms). Two groups of rats were given two different sets of experiences with these visual cues. One group was exposed to the cues and to the spatial relations among them by simply being placed in the visual environment (the laboratory room in which the maze was located) for large amounts of time both before and during maze training. A control group was given exposure to a different laboratory room but was prevented from having any visual contact with the room in which the radial maze was located aside from the restricted views available from within the maze.

If prior exposure to the spatial relations among the cues and locations in the extra-maze visual environment is important for producing representations

of spatial relations among the maze locations, and if such representations are important for supporting performance in the radial-arm maze, then the group exposed to the room containing the maze should learn to perform in the maze more rapidly (and/or perform at higher terminal levels) than the control group. Furthermore, the mechanism of any effect of spatial exposure should include enhanced spatial guidance of choices in animals that have experienced the spatial relations among cues and locations in the test environment.

METHOD

Subjects. The subjects were 20 male Sprague–Dawley rats obtained from Harlan Sprague Dawley, Inc. (Indianapolis, IN). They were approximately 4 months of age and experimentally naive when the experiment began. The rats were housed in groups of 3 or 4 in a colony room with a 12:12 light: dark cycle. They began a restricted diet of 13 g per day of Purina Rat Chow 10 days prior to the beginning of the experiment.

Apparatus. The apparatus was the same enclosed 8-arm radial maze used by Brown and Moore (1997). The central arena was an opaque refuse container (Rubbermaid, Inc., ''Roughneck''), which was 77 cm tall and 44 cm in diameter at the end used as the floor of the maze. Eight holes were evenly spaced (16 cm apart center-to-center) and centered 15 cm from the floor of the central arena. The floor of the central arena was formed by a 3-cm layer of bedding material. Eight 78-cm sections of white polyvinylchloride (PVC) tubing (10-cm interior diameter) were inserted into these holes, with the joints well caulked to ensure a light-proof seal. The tubes were supported by braces and attached to a wooden turntable (mounted on a ''lazy susan''), allowing the entire apparatus to be easily rotated relative to the room. A photograph of the apparatus is available in Brown and Moore (1997) and on the Internet at www.vill.edu/~mbrown/.

A critical modification of the maze from the earlier experiments of Brown and Moore (1997) was that visual information from the extra-maze environment was allowed to enter the terminal ends of the maze arms. From the rat's prespective, the end of each maze arm was formed by a wall of nylon mesh material. The mesh was made of very thin material, which did not obstruct the view of objects viewed through the mesh, at least to the human eye. This mesh wall was 18 cm from the end of the PVC tube forming the maze arm. Thus, the visual stimulus available to the rat at the end of each maze arm was spatially restricted by the remainder of the PVC tube, which extended beyond the mesh wall. In fact, the position of the mesh wall was chosen so that there was no overlap in the visual stimuli available from neighboring maze arms. Small black plastic containers (2.0 cm square and 1.5 cm deep, open at the top) were attached to the insides of these mesh walls and served as food cups. The mesh wall/food cup assemblies were attached to sections of smaller diameter PVC tubing (7.6-cm interior diameter), which

allowed them to be easily removed for baiting (or unbaiting) the food cups. A plywood sheet served as a removable lid for the apparatus. A hole in the center of this lid allowed the lens of a camcorder (mounted on the lid) to protrude into the maze. The camcorder's view was displayed on a monitor, thereby allowing the choices of the rats to be observed.

Two windows in the room were covered with opaque material to ensure that the only light in the room was from a bank of four fluorescent tubes mounted on the ceiling directly above the maze. During training and testing in the radial-arm maze, a white noise generator (San Diego Instrument Co.) was used to mask extraneous noise. To reduce the possibility that the noise might itself serve as a polarizing cue, the speaker was located directly above the center of the maze. Its effect was measured as 65 dB in the central arena of the maze.

Two enclosures were used to accomplish the primary experimental manipulation of exposing the rats to cues in two different laboratory rooms. The first enclosed the radial-arm maze described above. The enclosure was 220 cm square, with the maze in the center. Two walls were formed by walls of the room, and the other two were constructed from lumber and wire mesh (71 cm tall). The mesh was constructed of thin wire with 1-cm gaps, which obstructed the view of cues beyond the mesh wall only minimally, at least to the human eye. There was a floor-mounted air conditioning unit under the window, which was within the enclosed space. The entire room holding the enclosure and the maze was 3.6×4.4 m. In addition to the radial-arm maze used in this experiment, the room contained a second radial-arm maze, a lectern, several bookshelves, and chairs. There were a variety of posters and other visual cues on the walls of the room.

A nearby laboratory room held a second enclosure used in the Control Room exposure group (see below). The room was similar in size (3.3×4.4 m), with similar paint, flooring materials, and lighting. The enclosure was in a corner of the room, two sides of the enclosure being formed by the walls of the room and the other two by the same materials used in the experimental room. A plywood panel (122 cm long and 152 cm tall) formed a fifth wall of the enclosure by traversing the corner of the room. The walls, constructed of wire mesh, were 218 and 249 cm long. There was a large uncovered window on one wall of the enclosure. A circular refuse container was placed in the center of the enclosure. The remainder of the room contained several tables with a variety of equipment on them, a large laboratory bench with cabinets above it, and a variety of visual cues on the walls.

Room exposure. The rats were randomly divided into two experimental groups, which differed in terms of the rooms to which they were exposed. The Maze Room exposure group was given sessions of exposure to the room containing the radial-arm maze, whereas the Control Room exposure group was given daily sessions of exposure to the nearby laboratory room. Each group of rats was simply placed (together) in the appropriate enclosure for

1–4 h (except for one session which, by mistake, lasted 12 h). During exposure sessions, rats were free to (and did) explore the entire enclosure. In the Maze Room exposure group, this included climbing on (but not in) the maze and spending time in locations directly adjacent to the ends of the maze arms. Prior to any experience with the maze, there were 14 exposure sessions, occurring approximately 5 days per week, for a total of 43 h of exposure. These exposure sessions continued during maze training and the free choice trials (see below), for an additional 19 sessions and 44.5 h of exposure. Exposure sessions occurred immediately following free choice trials in the maze.

During each of 3 days prior to its first placement in the maze, each rat was given 10–20 of the 45-mg sucrose pellets (BioServe, Inc., Frenchtown, NJ) to be used in the experiment.

Maze training. One maze-exposure trial occurred the day of the 15th room exposure session. Prior to this trial, sucrose pellets were placed in each food cup and scattered along the length of each maze arm. Rats were placed in the center of the maze and allowed to explore the maze and consume pellets in groups of three or four rats (cagemates).

Rats were then individually trained to obtain pellets from the ends of the maze arms. Prior to each trial, the maze was rotated into one of eight equally spaced orientations, randomly chosen. Two pellets were placed in each food cup and 5–6 pellets were scattered along the surface of each maze arm. The rat was first placed in the central arena by opening the lid, placing the rat in the center of the central arena, and replacing the lid as quickly as possible. Rats were placed in the maze in a consistent spatial orientation. The rat was then allowed to choose from among the maze arms until all eight arms had been chosen or 10 min had elapsed. A choice was defined when the rat's entire body disappeared into the tube that formed a maze arm. Daily training trials continued until the rat consumed pellets from all food cups during a single trial.

During these training trials and during all the testing trials described below, all rats were carried into and out of the room for maze testing in an enclosed container (a flower pot 15.5 cm in diameter and 13.5 cm tall, covered with a small sheet of plywood). The container was opened only when the rat was inside the central arena of the maze and the rat was placed in the container before being removed from the maze following the trial. This was done to ensure that the Control Room exposure group was never exposed to the spatial cues in the testing room, except for the particular (and restricted) views available through the ends of tubes forming each maze arm. However, the experimenter was careful not to rotate the containers, to reduce any disruption of intertia-based orientation cues (Martin, Harley, Smith, Hoyles, & Hynes, 1997; Dudchenko, Goodridge, Seiterle, & Taube, 1997).

Free-choice trials. Daily test trials followed successful training and were identical to the training trials just described except that the maze was baited only with two pellets in each of the food cups and the trial was terminated

after all eight arms had been chosen or 5 min had elapsed without a choice. Fifteen trials were conducted for each rat.

Forced-choice trials. Each forced-choice trial consisted of two segments, separated by a short trial interruption. During the first (forced-choice) segment, the rat was forced to visit a randomly chosen set of four maze arms. During the second (free-choice) segment, the rat chose freely from among the eight maze arms. Only maze arms in spatial locations not visited during the forced choices were baited.

Prior to each forced-choice trial, the maze was rotated into one of the eight equally spaced orientations (randomly chosen). Four of the eight locations had been randomly preselected as the locations to which the rat would be forced. Those four maze arms were baited, and the remaining four were blocked, using inserts that fit into the junction of the central arena and maze arm (see Brown & Moore, 1997). The rat was then placed in the central arena (using the containers described above) and the lid of the apparatus was closed. The rat was allowed to choose from among the four available maze arms until each had been chosen. It was then removed from the maze and placed in a small cage, while the maze was prepared for the second (free-choice) segment of the trial. The brief delay was approximately 1–2 min in duration. During the delay, the maze was rotated into one of the eight orientations, randomly chosen with the constraint that the orientation used during the second (free-choice) phase of the trial not be the same as that used during the first (forced-choice) phase of the trial. In addition, the blocks were removed from arm entrances. The four maze locations not visited during the forced choices were baited.

Following the brief delay, the rat was returned to the maze. The orientation of the rat as it was returned to the maze was pseudo-randomized, in order to encourage use of the visual cues. The rats were then allowed to choose freely from among the eight maze locations until the four correct (baited) ones had been chosen. Behavior in the central arena during this free-choice phase of each trial was videotaped for later analysis. The rats were tested for seven forced-choice trials.

RESULTS

Free-choice trials. Choice accuracy during the free-choice trials was very high and did not differ in the two experimental groups. Figure 1 shows the mean number of choices required to finish the maze in the two exposure groups, during three blocks of five trials each. A Group $\times$ Block analysis of variance (ANOVA) confirmed that the number of choices declined over the course of trial blocks ($F(2,36) = 16.1$; a rejection criterion of $p < .05$ was used for all statistical decisions reported in this paper). However, there was no evidence for an effect of exposure condition ($F(1,18) < 1$) nor for an interaction between effects of Block and Group ($F(2,36) < 1$). The high levels of choice accuracy obtained in this experiment do not appear to be
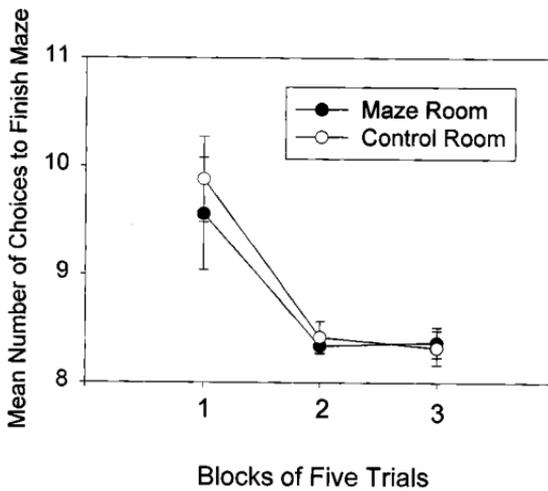
FIG. 1. The mean number of choices required to complete the maze during the free-choice trials for subjects in the two room exposure groups. Error bars represent standard errors of the mean.

attributable to consistent response patterning (e.g., consistently choosing the arm immediately adjacent to the last choice). Table 1 shows the movements from one maze location to the next in terms of the spatial separation between the two choices. These values include choices made during all 15 free-choice trials. There is not a high degree of consistency in choice-to-choice movements either within subjects or between subjects, and the magnitudes of tendencies to choose spatially proximal arms are similar to those found in experiments using standard radial-arm mazes (e.g., Olton, 1978).

Forced-choice trials. The rats' ability to selectively visit correct maze locations following the trial interruption (i.e., to visit maze arms in locations that had not been visited during the forced choices) was poor. The mean numbers of choices required to choose the four baited maze arms during the free choices of the forced-choice trials were 7.4 and 7.7 in the Maze Room Exposure and Control Room Exposure groups, respectively. These values are not reliably different ($t(18) = 1.31$).

To examine the control of choices by the spatial locations and the physical maze arms visited as forced choices, probabilities of visiting maze arms in each of four classes (one or more times) during the first four free choices following the trial interruption were determined. This measure has been used in our recent studies involving enclosed radial-arm mazes in order to separate control of choices by spatial location from control of choices by intra-maze cues, such as odor traces left during earlier visits (Brown & Bing, 1997; Brown & Moore, 1997). The four classes of arms were defined by whether or not the physical maze arm in that spatial location had been visited as a forced choice and whether or not the location had been visited as a forced

TABLE 1
Spatial Separations among Consecutive Choices in Free-Choice Phase

Subject	Spatial separation between consecutive choices				
	0	1	2	3	4
Maze room exposure group					
M-1	.02	.66	.20	.10	.02
M-2	.01	.12	.64	.18	.06
M-3	.02	.09	.63	.22	.05
M-4	.01	.21	.55	.17	.05
M-5	.01	.18	.48	.19	.14
M-6	.02	.47	.22	.18	.11
M-7	.02	.13	.52	.21	.12
M-8	.01	.06	.55	.26	.11
M-9	.01	.45	.32	.17	.04
M-10	.01	.45	.32	.17	.04
Control room exposure group					
C-1	.02	.08	.73	.15	.02
C-2	.01	.57	.31	.09	.02
C-3	0	.56	.29	.11	.05
C-4	.02	.11	.41	.30	.16
C-5	0	.51	.30	.12	.07
C-6	.01	.52	.21	.17	.10
C-7	.02	.85	.05	.06	.03
C-8	.01	.08	.59	.25	.06
C-9	.01	.15	.72	.08	.04
C-10	0	.60	.24	.09	.07

Note. There are two maze locations (arms) separated by 1, 2, and 3 from the previous choice, but only one maze locations separated by 0 or 4 from the previous choice. Values shown are the proportion of choices in each category.

choice. These probabilities are shown for each of the two experimental groups in Fig. 2. The probabilities were all close to that expected on the basis of chance (approximately .5, but not exactly .5 if the same location is visited more than once). The probability of revisiting physical maze arms that had been visited as a forced choice did not differ from the probability of visiting maze arms that had not been ($F(1,18) < 1$). The probability of revisiting spatial locations that had been visited as a forced choice did not differ from the probability of visiting spatial locations that had not been ($F(1,18) = 1.76$). Neither of these factors interacted with experimental groups ($Fs(1,18) < 1$).

In terms of these measures, subjects in the forced-choice trials of this experiment demonstrated no ability to avoid revisits to the locations to which they were forced during the first (forced-choice) part of the trial. However, more sensitive measures of discrimination ability in the radial-arm maze have been used in earlier experiments in our laboratory (e.g., Brown, 1992, 1993). These involve measuring the behavior of the rat as it explores the
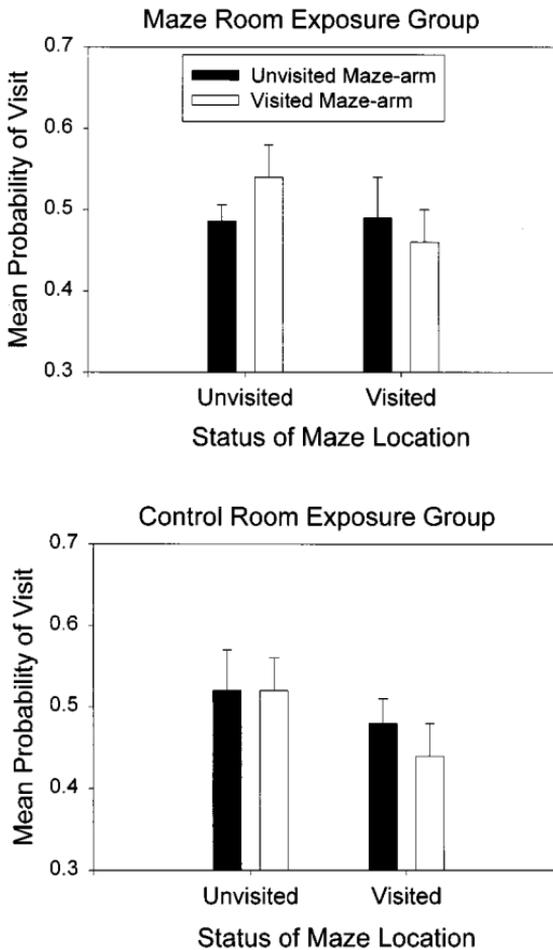
FIG. 2. The mean probability of visiting a maze arm during the first four choices following the trial interruption of the forced-choice test trials, as a function of whether the physical maze arm and the location of the maze arm had been visited during the forced-choice segment of the trial. These two factors were dissociated because the maze was rotated into a different orientation during the trial interruption. Data are shown for the Maze Room (top) and Control Room (bottom) exposure groups. Error bars represent standard errors of the mean.

entrances to the maze arms and (presumably) decides which one to visit. Easily identifiable observing responses can be measured, during which the rats hesitate at the threshold leading to a maze arm and appear to visually orient toward the stimuli available beyond the end of the arm. Brown (1992, 1993) argued that each of these observing behaviors corresponds to a spatial ''microchoice,'' during which the rat makes a go vs no-go decision with reference to that particular maze location. Thus, each microchoice results either in a visit to the arm (a ''macrochoice,'' which is all that is measured in most radial-arm maze experiments) or in the rejection of that maze arm.
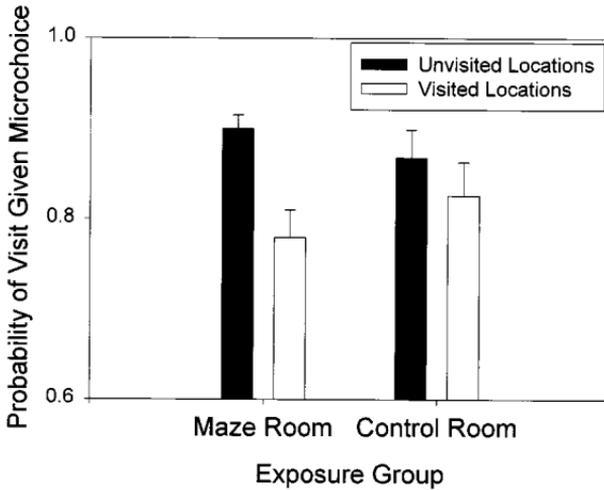
FIG. 3. The mean probability of visiting a maze arm following a microchoice during the choices that followed the trial interruption of the forced-choice test trials, as a function of whether that location had been visited during the forced choice and experimental group. Error bars represent standard errors of the mean.

The rejections provide behavioral information about spatial decision processes that is not commonly available.

The behavior of the rat in the central arena of the maze was recorded by the camcorder during the second (free-choice) segment of each forced-choice trial. These videotapes were coded by an observer who was not aware of the experimental hypotheses being tested nor of the group assignment of individual rats. He coded a ''microchoice'' whenever the snout of the rat entered the tube forming a maze arm. Sometimes these entries were followed by (or were part of) the full entry of the rat into the maze arm for a visit (macrochoice). Other times, the rat rejected (withdrew from) the maze arm following a microchoice. Figure 3 shows the probability of the rat visiting the maze location, given that a microchoice occurred for a location which the rat had visited during the forced choices or had not visited during the forced choices. Data are shown separately for the two experimental groups. Only the first microchoice directed toward a particular maze location was included in this analysis (because the effect of previous microchoices of the same location is unknown and potentially problematic). Rats were more likely to visit maze locations to which they had not been forced (and that were therefore correct) than to visit maze locations to which they had been forced ($F(1,18) = 19.8$). However, this effect was larger for rats in the Maze Room group than for rats in the Control Room group, as shown by an interaction between the effects of Group and Location type ($F(1,18) = 4.6$). There was no main effect of Group ($F(1,18) < 1$).

These microchoice outcome data can also be analyzed using measures

developed in the context of signal detection theory (e.g., Green & Swets, 1988), with the visits following microchoices directed toward correct maze locations being ''hits'' and the visits following microchoices directed toward incorrect maze locations being ''false alarms'' (Brown, 1993). A standard measure of discriminability based on signal detection theory is A' (Green & Swets, 1988). The mean values of A', based on the same data represented in Fig. 3, are .56 and .52 for the Maze Room and Control Room exposure groups, respectively. The values differ significantly ($t(18) = 2.15$). Rats in the Maze Room exposure group discriminated between locations to which they had been forced and locations to which they had not been forced at a higher level than expected by chance (chance $= .50$; $t(9) = 4.57$). The A' value for rats in the Control Room exposure group did not differ significantly from chance ($t(9) = 3.95$, $p = .065$).

A second analysis using these microchoice data looked for spatial guidance of choice behavior by identifying the target of microchoices: i.e., the identity of maze locations toward which the rat oriented, regardless of whether it then visited or rejected that location. If rats are spatially guided toward the location of correct maze arms, then correct (previously unvisited) maze locations should be the target of microchoices more often (and/or earlier in the trial) than incorrect maze locations (Brown, 1992, 1993; Brown et al., 1993). To investigate this, we determined the identity of the target of the first four microchoices following trial interruption (i.e., during the free-choice phase) of the forced-choice trials. We looked only at the first four microchoices because four microchoices is the minimum number that must be made in order to complete the trial. Furthermore, any microchoices of maze locations that had been the target of an earlier microchoice (earlier in the free-choice phase of the trial) were not counted. In the Maze Room exposure group, 47.1% of these microchoices were to correct locations (the expected value based on chance is 50%). The corresponding value for the Control Room exposure group was 51.5%. Thus, there is no evidence that subjects were guided toward correct locations to a greater extent in the Maze Room exposure group, nor indeed that either group was spatially guided to any extent.

DISCUSSION

If local views of the visual environment are integrated with information about movement paths to form a cognitive map, then one would expect massive prior exposure to the visual cues in the maze room during free locomotion in that room to facilitate spatial performance in that visual environment. There was no evidence for such an effect in the present experiment.

There was no effect of spatial exposure on acquisition of the radial maze task during the free-choice trials. Both groups acquired the task very rapidly and performed at very high levels of choice accuracy.

During the forced-choice test trials, there was no difference between the

performance of the experimental groups in terms of standard measures of choice accuracy. However, more sensitive measures of spatial choice revealed that rats in the Maze Room exposure group were slightly better able to discriminate previously visited arms from those that had not yet been visited. These more sensitive measures allow visual discrimination ability to be dissociated from spatial guidance (Brown, 1993), and the effect of spatial exposure on visual discrimination ability can be explained in terms of perceptual learning about the visual cues used in the discrimination. For example, Chamizo and Mackintosh (1989) showed that preexposure to cues used in a spatial discrimination facilitated discrimination learning, and they provided evidence that this could be explained in terms of a theory of discrimination learning that was developed to explain discrimination of visual stimuli very generally (i.e., the theory is not specific to spatial cues; McLaren, Kaye, and Mackintosh, 1989; also see Hall, 1991). Based on very different logic, Whishaw (1991) concluded that the enhanced ability of rats to navigate in the Morris Water Maze following preexposure to the spatial cues was best explained in terms of associative processes that are not particular to spatial abilities. Similarly, the present result that preexposure to visual cues enhances subsequent spatial discrimination ability is best explained in terms of perceptual learning about the visual cues available from the central arena of the maze.

In contrast to the difference in discrimination ability that was found, a difference in the extent to which rats in the experimental group were spatially guided to maze arms *would* constitute an effect of spatial exposure on processes that are specialized for spatial tasks (Brown *et al.,* 1993). However, there was no evidence that rats were guided toward the location of correct (baited) arms in either experimental group. Thus, the present results provide evidence for a small effect of prior exposure to spatial cues on the discriminability of visual cues used in choosing among maze arms, but no evidence for an effect of prior exposure on control by the spatial relations among the maze arms.

There is a growing consensus that spatial performance in animals can be controlled by the spatial relations among objects and locations in the environment, although the manner in which those relations control behavior and the conditions under which they are important determinants of behavior are matters of debate (for reviews, see Gallistel, 1990, and Poucet & Benhamou, 1997). The present results do not diminish the evidence for the existence of such representations. They do, however, speak to the issue of how such representations are acquired. As outlined in the introduction, several recent ideas about the acquisition of control by these spatial relations include the idea that self-generated movement among local views of the visual environment provide the information about spatial relations (Etienne *et al.,* 1996; Gallistel & Cramer, 1996; McNaughton *et al.,* 1996; Poucet, 1993; Benhamou *et al.,* 1995). In the apparatus used in the present experiment, spatial

relations among the maze arms were not perceptually apparent, because the views of the environment available from the maze arms did not overlap.[1] Thus, any representation of the spatial relations among extra-maze visual cues in the present experiment could only be obtained from the self-generated movements required to travel among places in the maze and its surrounding environment. The failure to find evidence for an effect of movement among the visual environment of the maze is therefore problematic for the idea that movement among local views is responsible for the development of representations of spatial relations. In the present experiment, rats that had only moved among local views available in the maze task itself performed at levels equivalent to that of rats that had massive experience moving in the visual environment of the maze.

An important limitation of the present results is the possibility that the rats in this somewhat unusual radial maze were controlled by the visual spatial cues only to a limited extent. In the same maze that was used in the present experiment, but with extra-maze cues unavailable (because the ends of each maze arm were blocked by an opaque cap), rats apparently rely on intrinsic (vestibular or kinesthetic) information (Brown & Moore, 1997). We expected that providing access to the extra-maze visual cues from each maze arm (albeit only small perspectives) would result in primary control of choices by those cues, at least in the Maze Room exposure group. The fact that exposure to the visual cues affected subsequent discrimination ability (as shown by the A' results) shows that the visual cues *were* involved in spatial choices to at least some extent. However, it is possible that the choice behavior of rats in the present experiment was controlled primarily by path integration rather than visual cues and that visual cues played a relatively minor role in the control of behavior in the present experiment. Thus, the small size of the effect of the experimental treatment (and the failure to find evidence for spatial guidance) may be due in part to limited use of visual cues in the present apparatus.

Consistent with the idea that control by extra-maze visual cues was limited is the fact that rats in the present experiment performed so poorly in the forced-choice procedure. In standard radial mazes (with free access to extra-maze visual cues) there is little or no disruption of choice accuracy by a forced-choice procedure relative to a free-choice procedure (e.g., Cook, Brown, & Riley, 1985). However, there now appears to be a consistent finding that, in mazes with restricted access to visual cues, choice accuracy is very much disrupted by a foced-choice procedure. Schenk *et al.* (1997) re-

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[1] There is an important *proviso* to this aspect of the experimental logic. It is possible that the similarity of the views available from the ends of maze arms might differ systematically as a function of spatial proximity, even though there is no explicit overlap in the cues available from adjacent arms (e.g., views from arms on one side of the room might be more similar to each other than to arms on the opposite side of the room).

cently reported an experiment using a maze that was very similar to the present one. They tested rats in a radial-arm maze in which visual cues were available only from the ends of the arms or (as is typical) were available throughout the maze. In the former group, choices were very accurate during free-choice trials, but substantially less accurate during a forced-choice procedure. Earlier eperiments from our laboratory using mazes with restricted access to extra-maze visual cues have also found this pattern of high levels of choice accuracy in a free-choice procedure, but not in a forced-choice procedure (Brown & Bing, 1997; Brown & Moore, 1997). It may be that restricting visual cues increases the relative control of spatial choice by intrinsic cues (i.e., by kinesthetic or vestibular cues and the path integration process that uses them; see Brown & Moore, 1997) or by intra-maze cues (Brown & Bing, 1997). The trial interruption required by the forced-choice process would be expected to be more disruptive of control by such intrinsic cues than of control by visual cues. On the other hand, it should be noted that less severe restriction of access to extra-maze visual cues has been found to increase the extent to which spatial relations among those cues control behavior (Brown *et al.,* 1993).

Although the conclusions following from this experiment must be tempered by the small size of the exposure effect and by the possibility that visual cues were involved in the discrimination to only a limited extent, the present results suggest that exposure to visual spatial cues affects spatial abilities only via perceptual learning processes that are common to other discrimination abilities. Thus, the present results provide no support for the idea that cognitive maps form when rats have an opportunity to combine local views of an environment with information about the movements necessary to get from one view to another.

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