Hippocampal Lesions Disrupt Navigation Based on the Shape of the Environment

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Geometric information provided by the walls of an environment has a strong influence over hippocampal unit activity. This suggests that the hippocampus forms part of a cognitive mapping system that encodes geometric relationships between environmental cues and the animal’s location. Here, the authors show for the first time that excitotoxic lesions of the hippocampus disrupt the ability of rats to navigate to a goal using shape information provided by a solid-walled arena and an array of identical landmarks. These results are consistent with cognitive mapping theories of hippocampal function and extend previous research by showing that hippocampal cell loss impairs navigation with respect to shape information provided by both physical barriers and an array of landmarks.

Several studies have shown that environmental features can influence the firing rates of hippocampal neurons (for review, see Poucet, Save, & Lenck-Santini, 2000; Wiener, Berthoz, & Zugaro, 2002). O’Keefe and Dostrovsky (1971) were the first to show that the pattern of electrical activity of pyramidal cells in the CA1 subregion of the hippocampus was related to the animal’s position in space. More recent research has shown that both proximal and distal visual cues can exert an influence over place fields in the hippocampus (Wiener et al., 2002; but see Cressant, Muller, & Poucet, 1997). Indeed, the barriers formed by the walls of a test environment can provide a powerful reference cue for place field orientation. For example, O’Keefe and Burgess (1996) found that place cells responded to distance information relative to the walls of an arena (see also Gothard, Skaggs, Moore, & McNaughton, 1996). Hippocampal place cells also respond differentially in different shaped environments (Muller & Kubie, 1987), and the place cell representation diverges spontaneously with repeated passive exposure to two different shaped arenas (Lever, Wills, Cacucci, Burgess, & O’Keefe, 2002). One possible interpretation of these findings is that the hippocampus encodes information about the shape of the animal’s environment. Such a representation is potentially important because it could form the basis of a cognitive map (see O’Keefe & Nadel, 1978), which has been defined as “a record in the central nervous system of the macroscopic geometric relations among surfaces in the environment used to plan movements through the environment” (Gallistel, 1990, p. 103; see also Lever et al., 2002; O’Keefe & Burgess, 1996).

Several studies have shown that animals including humans are able to use shape information to locate a hidden goal (e.g., rats: Cheng, 1986; Margules & Gallistel, 1988; Pearce, Ward-Robinson, Good, Fussel, & Aydin, 2001; pigeons: Kelly, Spetch, & Heth, 1998; chicks: Tommasi, Vallortigara, & Zanforlin, 1997; Vallortigara, Zanforlin, & Pasti, 1990; fish: Sovrano, Bisazza, & Vallortigara, 2003; nonhuman primates: Gouteux, Thinus-Blanc, & Vauclair, 2001; humans: Garrad-Cole, Lew, Bremmer, & Whitaker, 2001; Hermer & Spelke 1994, 1996). A number of these studies have also shown that animals and human children make geometric errors despite the presence of cues indicating the goal location (e.g., Cheng, 1986; Hermer & Spelke, 1994, 1996; Margules & Gallistel, 1988; but see Golob & Taube, 2002). In addition, studies of blocking (Kamin, 1969) and overshadowing (Pavlov, 1927) have shown that learning to locate a goal in a distinctive shape is not subject to the rules of cue competition typically seen in associative conditioning (Hartwick, Good, & Pearce, in press; Hayward, McGregor, Good, & Pearce, 2003; Pearce et al., 2001). These findings suggest that locating a goal with reference to shape information is acquired independently of alternative cue-based strategies that may also be used to locate a hidden goal. This conclusion is consistent with predictions derived from O’Keefe and Nadel’s (1978) cognitive mapping account of navigation and Gallistel’s (1990) geometric module theory of spatial learning.

Although unit activity suggests a role for the hippocampus in the processing of geometric information, the functional significance of these observations for navigation has not yet been explored. The main aim of the present study was to examine the effects of hippocampal cell loss on navigation to a hidden goal with reference to the shape of an environment. In Experiment 1, rats were required to find a submerged platform in a rectangular-shaped watermaze. Extramaze cues were obscured, and the arena was rotated between trials to preclude the use of extramaze cues to locate the platform. In Experiment 2, an identical procedure was used to examine navigation in a circular pool that contained four identical landmarks placed at the edge of the pool to form the shape of a rectangle. Control manipulations were carried out at the end of each experiment to determine whether rats with hippocampal lesions were able to use nongeometric information provided by

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the walls of an arena and the landmark array. According to a cognitive mapping account of hippocampal function, lesions of this structure should disrupt navigation with respect to shape information provided by either the walls of an arena (O’Keefe & Burgess, 1996) or an array of landmarks (Burgess & O’Keefe, 1996; O’Keefe & Nadel, 1978; see also Lever et al., 2002).

Method

Subjects

In both experiments, the subjects were 24 experimentally naive male Hooded Lister rats supplied by Joint Services, Cardiff University. The rats weighed 285–345 g before surgery and were given unrestricted access to food before and during the experiments. All the rats were housed in pairs in a room that was illuminated for 14.5 hr each day. The rats were tested for a minimum of 5 days a week during the light period of their diurnal cycle. There were two groups in each experiment. One group (n = 12) consisted of rats with ibotenic-acid lesions of the hippocampus (dentate gyrus and CA1–3), and the second (n = 12) consisted of rats subjected to a control operation. At the start of each experiment, one rat from each cage was randomly assigned to the lesion or to the control group.

Surgery

Each rat was anaesthetized using a mixture of isoflurane and oxygen and was then placed into a stereotaxic frame (Kopf Instruments, Tujunga, CA). The experimenter made an incision along the midline of the scalp and used a dental burr to remove the bone underlying the neocortex. Injections of ibotenic acid were made with a 2-μl Hamilton syringe (Reno, NV) mounted on the stereotaxic frame. The plunger of the Hamilton syringe was attached to an electronic microdrive (Model KDS 310; KD Scientific, New Hope, PA), which regulated the volume and rate of infusion of the neurotoxin. Ibotenic acid (Biosearch Technologies, San Rafael, CA) was dissolved in phosphate-buffered saline (pH 7.4) to produce a 63-mM solution and was infused (0.05–0.10 μl) at a rate of 0.03 μl/min at 28 sites (for stereotaxic coordinates of the injection sites, see Coutureau, Galani, Goselin, Majchrzak, & Di Scala, 1999). Following each infusion, the Hamilton syringe was left in place for 2 min to allow diffusion of the solution into the tissue and away from the injection needle. Rats in the sham-operated control group underwent a similar surgical procedure in which the skin was incised, the neocortex was exposed, and the dura was perforated with a 25-gauge Microlance3 needle (Becton Dickinson, Drogheda, Ireland), but no injection was given. The scalp incisions were sutured at the end of the procedure, and the rats were placed in a recovery box maintained at 40 °C for 3–4 hr. The rats with hippocampal lesions received a subcuneaneous 10-ml injection of saline and glucose solution. Once the rats had recovered sufficiently, they were transferred back to their home cages. A minimum of 14 days postoperative recovery was allowed before testing began.

Apparatus

Experiment 1

The apparatus was located in a room that was 4.0 m × 3.0 m and 2.3 m high. A circular pool, 2.0 m in diameter and 0.6 m deep, was mounted on a platform 0.6 m above the floor in the center of the room. The pool was painted white, made of fiberglass, and was filled with a mixture of water and 0.5 L of white food coloring E308 (Roehm & Haas UK Ltd., Dewsbury, UK) to a depth of 30 cm. The water temperature was maintained at 25 °C (± 2 °C). This pool was drained at the end of each day, cleaned, and refilled the following morning. A wide-angled video camera was fixed 1.75 m above the center of the pool, 5 cm above a 30-cm diameter hole in a white circular ceiling with a diameter of 2.0 m. The image from the camera was relayed to recording equipment and a PC running tracking software (Watermaze Software, Edinburgh, UK) located in an anteroom. Eight 45-W, 22.5-cm diameter spotlights were recessed into the circular hung ceiling. The lights were arranged at equal distances in a 1.6-m diameter circle with its center directly above the center of the pool. The spotlights were illuminated throughout the experiment. The pool was enclosed within a light blue curtain hung from the ceiling on a runner at a distance of 25 cm beyond the edge of the pool. The curtain was 1.4 m deep so that it hung from the ceiling to 20 cm below the rim of the pool.

A rectangular arena was created in the pool by inserting white polyurethane boards, 1.8 m or 0.9 m long, 0.59 m high, and 2 mm thick. The bars that supported the boards at the edge of the pool overlapped, causing the tops of adjacent panels to differ by 2 cm. The tops of the panels were thus either 33 or 35 cm above the surface of the water, although which panels (long or short) were lower in the water was varied randomly among sessions. The boards were placed in the pool to form a rectangular-shaped arena, the corners of which were in contact with the wall of the circular pool.

A clear Perspex platform, 10 cm in diameter and mounted on a column, was submerged 2 cm below the water surface in one of the corners of the rectangle. The center of the platform was 25 cm from the corner and 45° from each wall. A beacon could be attached to the platform 0.5 cm from its edge. The beacon was a black plastic rod, 1 cm in diameter and 15 cm high. It had a white plastic disc 3 cm in diameter and 0.5 cm thick attached to the top (see Figure 1).

To determine whether rats with hippocampal lesions were able to use featural information to locate the hidden platform in the absence of distinctive shape information, we used boards of equal length (1.41 m) to form a square arena at the end of training in the rectangular arena. Two of the boards were black and two were white. The details forming a square from these boards were identical to those used to form a rectangle.

Experiment 2

Experiment 2 was carried out in the same room and with the same apparatus with the exception that the four panels were replaced with an array of four landmarks. Each landmark was made from black polyurethane pipe, 1.18 m high and 67 mm in diameter. To stabilize the pipes, we attached each of them to weighted bases. Each landmark thus extended 0.88 m above the surface of the water and could be attached to the side of the pool by a bracket. The beacon was a plastic rod with the same dimensions as that used in Experiment 1 but with the exception that it was painted silver so that it was visible against the black drainpipes.

At the end of training with the black landmark array, we conducted control trials. To determine whether rats with hippocampal lesions could locate the hidden platform in an arena with distinctive rather than identical landmarks, we replaced two of the black landmarks with gray polyurethane sections of pipe with identical dimensions to those used previously.

Histology

After completion of behavioral testing, the rats were deeply anaesthetized using Euthatal (200 mg/kg sodium pentobarbitol) and perfused transcardially with physiological saline and 10% formol-saline. The brains were then removed and stored in formol-saline solution for at least 4 hr. The formol-saline was then replaced with 25% sucrose solution, and the brains were allowed to become saturated in the solution for 24–48 hr before being sectioned (40 μm), mounted on slides, and stained with cresyl violet.

Behavioral Procedures

Experiment 1: Navigation in a Rectangular Walled Arena

Stage 1. Rats were transported six at a time in 6 compartments of a light-tight carrying box that was placed on a bench in the southwest corner.
of the anteroom. The curtains were drawn around the pool throughout the experiment. All rats received 17 sessions of training in the rectangular arena. For the first 11 sessions of training, a beacon was attached to the platform. In subsequent sessions the beacon was removed. Each rat was trained for one session a day. Each session contained four trials in which the rat had to escape from the water by climbing onto the platform. For half the rats in each group the platform was located in Corner A, as shown in the upper panel of Figure 1, for a randomly selected two trials in each session, and for the other two trials it was located in Corner C—the geometrical equivalent of Corner A. The remaining rats were trained in a similar manner to find the platform in Corners B and D. The rats were lowered gently into the water facing the wall and were released once from each of the four sides in a random order within each session. For each training trial, experimenters used a stopwatch to record the time taken for a rat to reach the platform after release into the water. If a rat did not locate the platform within 90 s, the experimenter placed his hand about 5 cm in front of the rat’s nose and guided it toward the platform. After finding the platform, each rat was allowed to remain there for 30 s before being removed from the pool. The rat was then dried gently with a towel and returned to the carrying box where it waited until the remaining rats had received a single trial in the pool. After the 6 rats had each received a single trial, the rectangular arena was rotated ± 90°. The rectangle was always oriented along a north–south or east–west axis. This manipulation ensured that extramaze cues were redundant with respect to locating the platform and forced the rats to use intramaze cues.

For Sessions 12 to 17, the beacon was removed from the platform, and a record was taken of the first corner that a rat entered in each trial after being released into the pool. An entry into a corner was scored when the subject’s snout entered a zone defined by a circle with a radius of 15 cm, centered on the middle of the platform position, with two parallel tangents extending back to the walls on the arena so that they met the walls at 45° at a point 15 cm from the corner (see Figure 1). A correct choice was recorded if a subject entered a corner containing the platform or entered the corner in the diametrically opposite position. The two opposite corners of a rectangle are geometrically equivalent, and no distinguishing features were provided in the maze to discriminate between these locations. An incorrect choice was recorded if the subject entered a corner whose geometric properties were the mirror image of the correct corner.

In Session 17, the rats received three standard training trials followed by a test trial in which the platform was removed. Each rat was released from the center of the rectangle, and their swim paths were tracked for 60 s. The pool was divided into four equal quadrants for analysis, and times spent in each quadrant could be calculated for each rat. For each subject there were two correct quadrants, consisting of the quadrant containing the correct corner and the diametrically opposite one, and two incorrect quadrants, containing the two corners that had never contained the platform.

**Stage 2.** At the end of training in the white rectangle, the rats were transferred into a black and white square and trained to find the platform in one of the corners. Two black boards were placed opposite each other, as were the two white boards. Thus, the pattern of wall color in two diagonally opposite corners, E and G, was such that a black wall was on the right and a white wall on the left. In the remaining two corners, F and H, a black wall was located on the left and a white wall was located on the right. The platform was located in one corner of the arena in the same manner as in the previous stage. Thus, for half the subjects the platform was located in Corners E and G, and for the other half it was in Corners F and H. Selection of the corner that contained the platform was fully counterbalanced with respect to prior training in the rectangle. The beacon was attached to the platform for the first 10 sessions of training, after which it was removed for a further 6 sessions. Other aspects of the procedure were identical to those used for training in the rectangle. Individual escape latencies and first choices were recorded. In Session 16, the rats received three standard training trials followed by a test trial in which the platform was removed. Details of the test trial were identical to those described for the equivalent test trial in the rectangular arena.

**Experiment 2: Navigation in a Circular Pool With a Rectangular Array of Landmarks**

**Stage 1.** The rats were first trained to locate the platform with a beacon attached to it. They were trained in a circular pool with no landmarks present and the curtains drawn around the pool for four sessions. For the first trial, we placed the platform in one of the four quadrants of the circular pool, chosen at random, and released the rat from one of the four major compass points at the edge of the pool, chosen at random. Each rat received a training trial with the platform in a different quadrant and was released from a different compass point so that there was no pattern to the release points and platform position. The rats were simply required to use the beacon to locate the platform.

**Stage 2.** We then trained the rats with the landmark array. This phase of training was carried out in a similar way to that described for Experiment 1. All subjects were trained in the rectangular landmark array with the beacon attached to the platform for the first four sessions. The beacon was then removed for the remaining sessions. The rats were released from the edges of the circular pool from one of the four major compass points. In the present experiment, the choice zones were extended back to the edge of the circular pool, 15 cm from the center of the landmark on either side (see Figure 1). The center of the platform was 25 cm from the center of the
nearest landmark. The position of the platform relative to the rectangular array of four landmarks was determined in the same manner as for Experiment 1.

In Session 20, the rats received three standard training trials followed by a test trial with the platform removed. As in Experiment 1, we released each rat from the center of the pool and tracked its path for 60 s before we removed it from the pool. Search zones were set up using the tracking software to determine the amount of time each rat spent near the potential platform positions. These were four circular areas 20 cm in diameter, with their centers located 25 cm from the center of a landmark on an imaginary line that bisected the right angle created by the landmark and its two adjacent neighbors. There were two correct zones, which were adjacent to the landmarks that were near the platform during training, and two incorrect zones, which were adjacent to the landmarks that never had the platform near them.

Stage 3. To determine whether rats with hippocampal lesions could use distinctive features of the landmark array (the hue of the drainpipes) to navigate to a hidden goal, we replaced two black landmarks, which had occupied the previously nonreinforced corners of the arena, with similar gray landmarks. If rats with hippocampal lesions were impaired in processing the landmarks, then one would predict a deficit in using the distinctive features of the landmarks to find the hidden goal. All subjects received two sessions of training with the black and gray landmark array.

Results

Histology

The maximum and minimum extent of the lesions from Experiments 1 and 2 are shown in Figure 2. Four rats with hippocampal damage from Experiment 1 and one from Experiment 2 showed less than 50% cell loss and were excluded from the analysis. The remaining lesioned rats (Experiment 1, n = 8; Experiment 2, n = 11) showed 70%–100% damage to the hippocampal subfields bilaterally. All rats sustained near complete cell loss in the CA1/CA3 region. There was some minor sparing of the cells in the dentate gyrus in three subjects, but in all of these cases the cell loss in the remaining subregions was 90%–100% complete. The majority of rats also sustained cell loss to the ventral subiculum (including pre- and parasubiculum), although this damage was minimal or absent in more dorsal regions (approximately 6.6 mm from the brain surface). However, there was no detectable damage to medial or lateral entorhinal cortex in any of the lesioned rats.

Behavior

Experiment 1

Stage 1. For the initial training with the beacon attached to the platform the escape latencies provide a more sensitive indication of performance than the choice measure, because subjects swim directly to the beacon for the majority of the trials. The upper panel of Figure 3 shows the mean escape latencies for rats with hippocampal lesions and sham operated rats during the first stage of training with a beacon attached to the platform. Although lesioned rats took longer to reach the platform at the beginning of training, there was no difference between the groups by the end of training. An unpaired t test using individual mean latencies from the final three training sessions with the beacon attached to the platform showed there was no difference between the groups, t(18) = 1.58, p > .05.

The mean percentages of trials in which subjects swim directly to a correct corner for each of the remaining sessions are shown for both groups in the middle panel of Figure 3. From the outset of training without the beacon, the control rats swim directly to a correct corner on the majority of trials but the lesioned rats failed to develop a preference for the correct corners over the incorrect corners. An analysis of individual mean percentages of trials in which a correct corner was chosen first, collapsed across the training sessions without a beacon, revealed a significant difference between the groups, U(n1 = 8, n2 = 12) = 0.50, p < .01.

The results of the test trial with the platform removed are shown in the lower panel of Figure 3. An unpaired t test showed that control rats spent significantly more time in the correct quadrants than did lesioned rats, t(18) = 15.99, p < .01. Furthermore, one-sample t tests showed that although control subjects spent significantly more time in the correct quadrants than would be expected by chance, t(11) = 6.82, p < .01, rats with hippocampal lesions were not able to discriminate between correct and incorrect quadrants, t(7) = 1.31, p > .20.

Stage 2. Following transfer into the square arena, we trained the rats with a beacon attached to the platform. The upper panel of Figure 4 shows escape latencies for lesioned and control rats during the beacon phase of training. By the final three sessions of training, there was no difference between the groups in latency to find the platform, Sessions 8–10: t(18) = 1.97, p > .05.

The mean percentages of trials in which subjects swim directly to a correct corner without a beacon placed above the platform are shown in the middle panel of Figure 4. Following removal of the beacon, both lesioned and control rats swim directly to a correct corner on the majority of trials. Analysis of the mean proportion of trials in which a correct corner was chosen first, collapsed across training trials without a beacon, revealed no significant difference between the groups, U(n1 = 8, n2 = 12) = 41.5, p > .05.

The results of the test trial with the platform removed are shown in the lower panel of Figure 4. Inspection of this figure reveals that there was no difference between control and lesioned rats in the percentage of time spent in the correct quadrants of the black and white square (t < 1). Furthermore, both lesioned and control rats spent more time than expected by chance in the correct quadrants, lesioned rats: t(7) = 76.96, p < .01; control rats: t(11) = 79.73, p < .01.

Experiment 2

Stage 1. The mean escape latencies for lesioned and control rats to climb onto the platform indicated by a beacon (Sessions 1–4) are shown in the left portion of the upper panel of Figure 5. Although lesioned rats took longer than controls to reach the platform at the beginning of training, an unpaired t test showed that there was no difference between the groups by the final two sessions, ts(21) < 1.62, ps > .11.

Stage 2. The mean escape latencies for each group during the second training stage in the rectangular array of landmarks and with the beacon attached to the platform (Sessions 5–8) are shown in the right portion of the upper panel of Figure 5. As in the previous training stage, lesioned rats took longer to reach the platform at the beginning of training, but there was no difference between the groups by the final training session (t < 1).
When the beacon was removed, lesioned rats did not demonstrate a preference for the two correct zones over the incorrect ones, whereas control rats developed a clear preference by the end of training (see Figure 5, middle panel). Analysis of individual mean percentages of trials in which a correct zone was chosen first, for the final six sessions combined, revealed a significant difference between the groups, $U(n_1 = 11, n_2 = 12) = 31.0, p < .05$.

The test trial without the platform present confirmed the conclusions drawn from the above analyses (see Figure 5, lower panel). A two-way analysis of variance (ANOVA) of individual

Figure 2. Histology from Experiments 1 (left) and 2 (right). The maximum (gray) and minimum (black) extent of the hippocampal lesions are shown at horizontal sections taken through the dorsoventral extent of the brain. The depicted sections are in millimeters from bregma (clockwise from top left: 3.1, 3.6, 5.6, 7.6, 8.6, 6.6, and 4.6) and are adapted from those in The Rat Brain in Stereotaxic Coordinates, G. Paxinos and C. Watson, Figures 91, 96, 99, 103, 107, 111, 113, copyright 1986, with permission from Elsevier.
Figure 3. Upper panel: Mean escape latencies for the two groups in Experiment 1 during training with a stick attached to the platform in the rectangular arena. Middle panel: Mean proportion of correct choices for the two groups during sessions with no stick attached to the platform in the rectangle. Lower panel: Mean percentage of time spent in the correct quadrants of the rectangle for the two groups in Experiment 1 during the test trial at the end of Session 17. Error bars represent standard error of the mean. HPC = hippocampus.
Figure 4. Upper panel: Mean escape latencies for the two groups in Experiment 1 during training with a stick attached to the platform in the black and white square arena. Middle panel: Mean proportion of correct choices for the two groups during sessions with no stick attached to the platform in the black and white square. Lower panel: Mean percentage of time spent in the correct quadrants of the black and white square for the two groups in Experiment 1 during the test trial at the end of Session 16. Error bars represent standard error of the mean. HPC = hippocampus.
Figure 5. Upper panel: Mean escape latencies for the two groups in Experiment 2 during training with a stick attached to the platform in a circular pool (Sessions 1–4) and in the rectangular array of landmarks (Sessions 5–8). Middle panel: Mean proportion of correct choices for the two groups during sessions with no stick attached to the platform in the rectangular array of landmarks. Lower panel: Mean percentage of time spent in the correct and incorrect search zones in the rectangular array of landmarks for the two groups in Experiment 2 during the test trial at the end of Session 20. Error bars represent standard error of the mean. HPC = hippocampus.
The aim of the experiments in this study was to assess the role of the hippocampus in navigating to a hidden platform whose position could be identified by referring to the cues provided by the shape created by four walls or four landmarks. The results showed that control subjects were able to identify the correct corner of both a solid-walled rectangular arena (Experiment 1) and a rectangular array of identical landmarks (Experiment 2). The rats were able to identify the correct corners only by referring to the cues defining the shape of the arena or the array. There were no additional cues available within the water maze, and distal cues from outside the pool were irrelevant with respect to the platform location. In contrast, rats with lesions to the hippocampus were not able to identify the correct corners by referring to information provided by the shape of either the arena or a landmark array. These results replicate earlier studies in showing that normal rats are able to use cues generated by the shape of a rectangular arena to find a hidden goal (Cheng, 1986; Margules & Gallistel, 1988) and extend their generality to a rectangular array created by four landmarks. A similar pattern of results was recently reported by Garrad-Cole, Lew, Bremner, and Whitaker (2001), who showed that young children were able to use the shape of a landmark array to find a hidden goal.

Control manipulations at the end of each experiment showed that lesioned rats were, however, able to discriminate between correct and incorrect corners of an arena or a landmark array if a visual feature specified the location of the platform. In Experiment 1, following training in a rectangular-shaped arena, the rats were transferred to a black and white square. The shape of the arena could not be used to identify which corner contained the platform, but subjects could use the hue of the walls to identify the correct corner. Rats with hippocampal lesions were unimpaired when tested in this apparatus, suggesting that they were able to use cues placed on the walls of an environment to locate the platform. Similarly in Experiment 2, following training with four black landmarks, we replaced the two landmarks specifying the incorrect areas in the rectangular-shaped array with gray landmarks. Rats with hippocampal lesions were then able to identify the area containing the platform just as well as control subjects. The fact that both groups were able to identify the correct zones following the replacement of black landmarks with gray ones may reflect nothing more than a tendency for animals to approach a familiar rather than a novel landmark. This strategy would lead animals to search near the landmark close to the platform or the diametrically opposite landmark. However, these results, together with those from training in a black and white square, are important for two reasons. First, they show that the deficits shown by rats with hippocampal lesions in the rectangular solid-walled arena and landmark array were not due to some theoretically uninteresting reason such as a difficulty in swimming or grossly impaired visual processes. Second, they show that rats with hippocampal lesions are able to find the platform when its position is indicated by a distinctive visual feature, such as the edge between a black and white wall or differences in the hues of landmarks. The results show unambiguously that rats with damage to the hippocampus are impaired in navigating to a goal location using cues provided by a rectangular arena or landmark array.

A number of experiments have examined how navigation in an arena with a distinctive shape is affected by the presence of cues located near the goal. Even though the cues may provide more reliable information about where the goal is located, it is generally found that their presence does not prevent animals from referring to the shape of the environment to find the goal (e.g., Cheng, 1986).

However, one factor that has been proposed to influence the extent to which rats use shape information to navigate to a goal location is the nature of the reinforcer. Golob and Taube (2002) trained rats to find a submerged platform near a distinctive landmark in a rectangular Morris pool and reported that the corner diagonally opposite to the platform was rarely approached. In contrast, when rats were trained in a similar task but with food as the hidden goal, they did not demonstrate a significant preference for the corner containing food over the diagonally opposite corner. Golob and Taube suggested, therefore, that rats adopt one type of navigational strategy when searching for food and another type when escaping from a Morris pool. If this suggestion is correct, then it is conceivable that the conclusions drawn from our experiments apply only to aversive procedures. However, the experiment by Golob and Taube was based on a working memory task, whereas our experiments involved a reference memory design. Moreover, there are good reasons for believing that the nature of the reinforcer is not critical for determining the outcome of reference memory tasks, at least those in which animals must find a hidden goal beside a landmark in one corner of a rectangular arena. Cheng (1986), using food as the goal, and Hayward, Good, and Pearce (in press), using a submerged platform as the goal, have found that rats perform quite similarly on these tasks. In both cases, rats eventually headed directly for the corner containing the goal on virtually every trial, but, during the acquisition of this response, they made errors of searching in the corner that was diagonally opposite to the correct corner. There were very few errors in either experiment of searching in the remaining two corners. Therefore, the pattern of performance of rats tested in the watermaze (aversive) procedures used in our studies show a parallel with the appetitive procedures reported by Cheng.
Given this type of result, Cheng (1986) and Gallistel (1990) have proposed that there is a module in the brain that is dedicated to processing geometric information, such as that relating to the shape of the environment. An important property of this module is that it is assumed to be impervious to other types of information so that spatial learning based on geometric properties will be unaffected by learning that takes place about other cues. According to O’Keefe and Nadel’s (1978) theory, animals create a cognitive map of an environment as they explore it. The formation of this map is not governed by an error-correction principle (e.g., Rescorla & Wagner, 1972). Instead it is governed by a mismatch detection mechanism whereby new cues are incorporated into the map as soon as they are encountered. According to both of these views, therefore, there is something special about spatial learning because it takes place despite the presence of other cues. The results from the experiments described here extend this conclusion by suggesting that the processing of geometric information with respect to navigation is disrupted by damage to the hippocampus (see also O’Keefe & Nadel, 1978).

A related reason for believing that there is something special about learning based on the shape of the environment comes from experiments that have examined the rate of firing of hippocampal cells while an animal explores its surroundings. The pattern of firing of hippocampal neurons (place cells) correlates with an animal’s position in its environment. Lever et al. (2002) showed that after passive exposure to two differently shaped environments, hippocampal place cell activity was correlated with the shape of each arena. According to O’Keefe and Burgess (1996), one of the features of the environment that strongly influences place cell activity is the distance of the animal from the wall of an arena. Individual place cells encode the location of the animal from the edge of an arena in the form of a Gaussian distribution with the peak level of activity located at a fixed distance from the arena wall. Burgess and O’Keefe (1996) further postulated that the hippocampal representation of environmental boundaries would generalize to other environmental features including landmarks (see also Hetherington & Shapiro, 1997). To our knowledge, the experiments described in the current article provide the first demonstration that an intact hippocampus is necessary to accurately navigate to goal locations within both a rectangular walled arena and a rectangular-shaped array of landmarks. The results from the present study therefore complement evidence from single-unit recording from hippocampal neurons in showing that damage to the hippocampus disrupts navigation based on cues provided by the shape of an environment. It should be noted that a potentially important difference between the methodology used by O’Keefe and Burgess and the present experiments is that polarizing cues provided by the experimental room were visible from the test arena in O’Keefe and Burgess’s study, whereas this was not the case in the present experiments. Nevertheless, our results extend previous research by showing that hippocampal cell loss affects a rat’s ability to locate a goal whose position is defined by the geometric relationships between individual landmarks.

The exact nature of the role played by the hippocampus in processing shape information requires additional research, and several questions remain to be addressed. For example, does the hippocampus contribute to the actual formation of a geometric module? This seems unlikely, as Golob and Taube (1997) found that in animals with hippocampal lesions, cells in the postsubicular-


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