THE ROLE OF THE HIPPOCAMPUS IN SPATIAL NAVIGATION IN THE RAT

By

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SUMMARY

In this thesis, I have addressed two main issues regarding navigation in rats. The first of these is the question of how rats use information provided by the walls of a distinctively-shaped environment to orient; more specifically, I have attempted to evaluate the claim that they do so by forming a mental representation of the global shape of the environment (Cheng, 1986). This claim was tested by training rats to locate a submerged platform in one corner of a rectangular swimming pool.

The second issue I have addressed is the assessment of the contribution made by the hippocampus towards the process of navigation. Experiments examined the effect of hippocampal lesions on the ability of rats to use the shape of their environment to locate a hidden goal. More specifically, the aim of the experiments was to test the proposal that the hippocampus is the site of a global representation of the environment. The experiments indicated that the hippocampus has a critical role in navigation with reference to the shape of an environment, but that this role is unlikely to be based on a global representation. I propose that the tasks on which hippocampectomized rats show a deficit are dependent on the use of local metric properties of the environment, rather than global ones.

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CHAPTER ONE - INTRODUCTION

Navigation is essential to the survival of many, if not all animals. Some birds seasonally migrate over long distances, only to return to their origins. Many animals store food and must be capable of knowing where that food is in order that they can return to it later. And any animal that has a nest must remember how to get home. Accordingly, diverse and ingenious methods of navigation have arisen across a range of species in order to cope with an assortment of situations.

Dead reckoning, for instance, involves the integration of all direction and distance information on an outward journey so that the animal can return directly to where it started its journey (Etienne, Berlie, Georgakopoulos, & Maurer, 1998). Dead reckoning is particularly useful when landmarks are sparse or imperceptible, such as when an ant forages for food in an open plain and needs to return to a nest site. When landmarks are available, these provide obvious cues to navigation; a landmark situated immediately adjacent to a goal site is referred to as a beacon (Gallistel, 1990), and location of the goal simply by moving towards this beacon is known as homing. When stimuli lie some distance from the goal, they can still be used to navigate, by knowing the spatial relationship between them and the goal. Gallistel calls this method piloting. Although piloting can be performed effectively when the cues are discrete landmarks (e.g. Morris, 1981; Roberts & Pearce, 1998), several recent experiments have placed an emphasis on navigation when the cue (or set of cues) is provided by the shape of the environment itself.

The material presented in this thesis is concerned with two main issues regarding navigation. The first of these is the question of whether or not animals possess a global representation of their environment (e.g. Cheng, 1986; O'Keefe and Nadel, 1978). To assess this, I will consider evidence from experiments in which animals were required to learn about the shape of their environment. This ability is of direct relevance to the question of whether animals use global cues to navigate. I will evaluate the extent to which a global representation may account for the available data, and outline alternative explanations for how this type of learning may progress.

The second issue addressed here concerns the hippocampus, and a possible role for this structure in navigation. The hippocampus has previously been implicated in the use of global cues (O'Keefe and Nadel, 1978), and a wide range of spatial deficits have been observed following hippocampal lesions. Where the use of global information can be demonstrated, it should be possible to show that animals with damage to the hippocampus are impaired at using these cues.

Navigation in an environment with a distinctive shape.

It has been suggested that animals possess a dedicated module for encoding information about the global geometric properties of their environment. This 'geometric module' was first proposed by Cheng (1986), and has been used to explain results in a diverse array of species. These results are reviewed in the following section, in which I will summarise the evidence that animals are able to use the geometric properties of their environment for orientation. I will then attempt to evaluate the extent to which this evidence allows us to conclude that a global geometric representation governs the use of this information.

From an evolutionary point of view, there are clear reasons why a geometric module might be of use. Gallistel (1990) discusses these reasons, pointing out that nongeometric information in most natural environments is inherently transient and therefore not sufficiently reliable for navigation over a long period of time. In food storing birds, for example, the positions of food caches need to be stored in memory in the autumn but retrieved in winter when the landscape may look very different. The large-scale shape of an environment, however, is far more permanent - it is made up of boundaries such as mountains and rivers, which are not ordinarily subject to the same kind of changes that affect feature information. One disadvantage of this method of orientation is that the shape of an environment as defined by large geological features necessarily covers a large area, which should lead to greater difficulty in accurate localisation of places in the absence of other information. Nevertheless, based on permanency of information, Gallistel concludes that "it makes biological sense that animals should orient themselves on the basis of the macroscopic shape alone" (Gallistel, 1990, p. 212).

Numerous studies (e.g. Cheng, 1986; Pearce, Ward-Robinson, Good, Fussell, and Aydin, 2001) have demonstrated animals' use of information provided by the shape of an environment in a laboratory setting. In most of the experiments described in this first section, animals were trained in a rectangular environment and required to find a hidden goal located in one corner. Location of the goal was possible only by reference to the walls of the environment, with measures taken by the experimenter to ensure no other strategy could be used. The measures included occlusion of extramaze cues by a curtain or barrier, reorientation of the test environment in relation to the wider environment in which it was located, disorientation of the animal (for example, by a period of rotation), or any combination of these methods. As a result, animals could only rely on information provided by the shape of the environment, together with any additional intramaze features provided by the experimenter. The information provided by the shape of the environment is frequently referred to as geometric information, and includes information about lengths of walls, angles between walls, the arrangement of walls at a particular corner, and the overall shape of the environment. Additional feature information is most commonly provided by visual features such as distinctive panels fixed to the walls, landmarks within the environment, or different coloured walls. Animals placed into an environment may orient according to information provided by the shape of the environment, feature information, or both – depending on the cues available in each particular instance.

In the case of a rectangular environment, defining a location according purely to geometric information gives rise to ambiguity. Any given location or corner is identical to an opposite twin in terms of geometric information; consider the rectangle shown in Figure 1. Corner A in this rectangle is formed by the conjunction of a short wall to the left of a long wall, and the same is true of the opposite corner, C. Likewise,

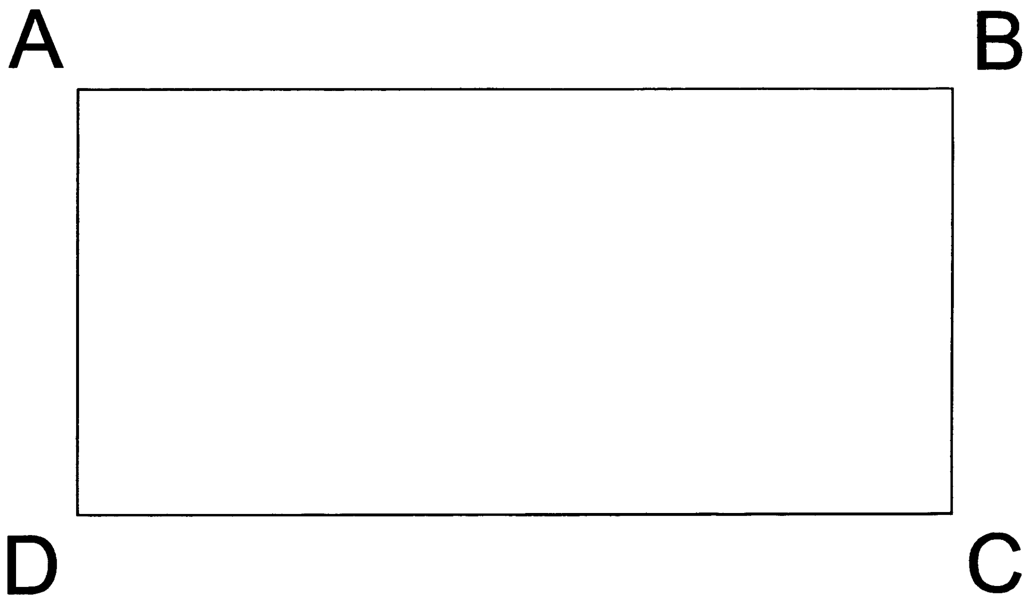

Figure 1. Schematic overhead view of a rectangular test environment.

corners B and D have the same arrangement of walls. Any specification of a corner based on geometric information, therefore, applies just as readily to the opposite corner. In situations where no additional feature information is available and an animal must orient according to information provided by shape alone, each corner is indistinguishable from its opposite partner – which leads to ambiguity in defining a location. In many of the experiments described in this chapter and throughout this thesis, however, feature information was present which disambiguated geometrically identical locations. Suppose, for example, that corner A contained a black landmark and corner C a white one. Although an animal would be unable to distinguish between these two corners on the basis of information provided by the arena's shape, it may be readily able to distinguish between them on the basis of the colours of the different landmarks they contain.

When animals are trained to find a hidden goal located in one corner of a rectangular arena, their performance is commonly assessed by recording choices. These are visits to the corners of arena made by the animals. If an animal visits a corner in which the goal is located, it is considered to have made a correct choice. Of course, animals do not always make correct choices. Rather, they are prone to making mistakes. For the most part, these errors decrease as training progresses and the animal learns the task. Before describing individual studies, it is worth drawing attention to a particular type of error made by animals – the 'rotational error'. This type of error is that which occurs when an animal makes a choice at the corner opposite the correct corner when feature information capable of disambiguating the two is present, and is termed a rotational error because this corner is located at a 180 ° rotation through the centre of the rectangle from the correct location. Rats making a rotational error are those visiting a corner which is geometrically correct, but incorrect in terms of feature information. Rotational errors are important for reasons that will be explained later, but it is worth paying attention to the occurrence of these choices in the studies that follow.

In a PhD thesis, Cheng (1984, described in Gallistel, 1990) reported two experiments conducted in an X-maze; a rectangular enclosure containing four arms in the form of an elongated X, with each arm running from the centre of the rectangle to one of its corners. At the end of each arm (i.e. at each corner of the rectangle) was a stimulus panel, a visual cue that varied from corner to corner. In the first experiment, the correct corner was baited with 18 food pellets, and the opposite corner with 6. The corner located adjacent to the correct corner along one of the shorter walls of the rectangle was baited with a single pellet, and the remaining corner was unbaited. Rats were released from the centre of the maze, and allowed to move freely within the arms to find the food. It was expected that during the course of acquisition the rats would learn to visit the correct corner first, followed by the opposite corner, in accordance with the quantities of bait placed at the ends of each arm. This was not the case. Although rats learned to visit these two corners more frequently than the remaining two, no rat successfully demonstrated an ability to make a higher number of visits to the correct than the opposite corner; presumably as a result of rats using geometric information but not features. In subsequent test trials, the stimulus panels were moved so that their positioning with respect to the corners of the rectangle was different. For the first test trial, each panel was moved to the corner opposite its original location. This transformation was equivalent to a 180 ° rotation of the available cues, and was designed to test the notion that the rats oriented according to a feature of the test space that the experimenters had not intended. Rats' arm choices were unaffected, and they continued to visit the two corners which were geometrically and featurally correct more often than the remaining two corners. In the second test, each panel was moved one position clockwise around the edge of the rectangle, preserving the sequence of panels but changing the relationship between each panel and the rectangular shape of the environment. The third test trial involved swapping the panels at opposite ends of each long wall, a transformation which altered both the order of panels and the relationship between each panel and the rectangular shape. Panels in each of these latter two test trials were located at corners with different geometries and arrangements of walls to the corners at which they were located during training. Performance on these test trials was equivalent to chance, with rats visiting the four corners equally. If these rats took no account of geometric information, we might have expected them to visit the corners in which those panels which had previously been associated with food were located. Likewise, if they did not use feature panels and relied solely on the geometric information, we might have expected them to search in the corners which preserved the geometric properties of the larger baits. That they did neither, and instead divided their choices between all four corners, suggests that the rats were sensitive to geometric information and the feature panels in the corners.

In a second experiment, rats were trained in a similar maze with food baits located at the end of one arm only. In this experiment, all rats learned to find the correct corner on at least 50 % of trials (the level achievable by relying on geometry alone), and four out of six rats learned to choose the correct arm at least 75 % of the time. This performance is above the level we would expect if rats were relying purely on geometry, and demonstrates the use of feature information. However, the results of test trials again showed that the rats were sensitive not only to features but also to the geometric properties of the corners. In test trials in which the panels were moved to corners with different geometries, performance was reduced to chance levels. If rats had learned to find the food based only on the identities of feature panels, moving those panels into new locations in relation to the shape of the environment should not have impacted upon their accuracy. That rats searched close to the correct feature less often when it was in a novel geometric position suggests that they were sensitive to some properties of the environmental shape. This again shows that rats were able to use information provided by the shape of the environment during training.

A slightly different paradigm was used by Cheng (1986). Rats were trained to find food in a rectangular environment, in two types of experimental procedure. The first of these was a working memory design, in which rats were required to find food hidden at a given location in a rectangular environment before being placed into an identical second arena and required to search at the equivalent location in order to find a food reward. On each pair of trials, a new location was used – in the second trial of each pair, therefore, the only information relevant to finding the food was the location of the reward during the exposure trial occurring immediately beforehand. The apparatus was a rectangular box, with distinctive feature panels located in each corner. In one version of the task, all four walls were the same colour; in another, three were black while one of the longer walls was white. In either case, feature information was available in addition to the information provided by the shape of the environment.

With regard to the environmental shape only, every location (except the centre of the arena) was indistinguishable from a second, geometrically equivalent location. This was due to the symmetry of the rectangle. In order to disambiguate the two, therefore, distinctive feature information had to be used. If rats searched for food during the second trial of each pair at the correct location, and did so reliably more than they searched at its rotational equivalent, we might conclude that they were not reliant solely on the information provided by the shape of the environment; but that they took account of the feature information provided by corner panels (and, where relevant, the distinctive white wall). This was not fully supported by the data. On each trial, a record was taken of the location at which the rat first dug to search for food. For classification, a dig was counted as correct if it occurred within 15 cm of the target location, and classed as a rotational error if it occurred within 15 cm of the rotational equivalent of the correct location. These circular choice zones each encompassed 10 % of the arena floor. In the version of the task with all four walls the same colour, rats chose the correct location on 47 % of trials, and the rotational equivalent on 31 % of trials. With a distinctive wall present, they searched at the correct location on 44% of trials and at the rotational equivalent on 25 % of trials. There are several important features to these data, the first of which is that rats chose the correct location and its rotational equivalent significantly more often than would be expected by chance. The second is that, although a slight numerical difference was apparent, there was no significant difference between correct choices and rotational errors. In sum, these findings suggest that rats relied primarily on information provided by the shape of the arena. Distinctive feature information was less important, although it is likely that it was used to some extent. Every rat chose the correct location more often than its rotational equivalent, suggesting at least some use of features to disambiguate geometrically identical places. Nevertheless, the rectangular shape of the environment seemingly provided the primary basis for orientation.

In a reference memory version of this task, rats were trained to find food hidden in one corner of a rectangular box. Each corner contained a bottle of food, which could be knocked over by the rat. Food from one bottle, always located in the same corner, would spill when the bottle was knocked over. Others were fitted with invisible caps that prevented the rats from gaining access to the food. Rats had to choose the correct rather than the incorrect bottles, and had to do so by reference to the walls of the arena. Once again, feature information of the type used in the working memory paradigm was present in addition to the information provided by the rectangular shape of the environment. During training, a record was taken of which bottle was knocked over first. Once again, rats chose the correct or the opposite corner more often than would be expected by chance. In contrast with the working memory experiment, however, they also distinguished accurately between the correct corner and its rotational equivalent. During the final 30 training trials and subsequent test trials carried out in the same conditions, rats chose the correct corner first on 71 % of trials and the opposite corner on 21 % of trials. The proportion of errors at the opposite corner was greater than at each of the other two incorrect corners; a pattern which can only be as a result of rats using information provided by the shape of the environment, as this is the only regard in which the opposite corner was 'more correct' than the other incorrect corners. Therefore, despite rats' use of feature information to disambiguate the two geometrically equivalent corners, the results of this reference memory task again suggest that rats learned about the position of the goal in relation to the shape of the environment.

In all of Cheng's experiments reviewed here, rats showed that they were able to learn about the position of a hidden goal in relation to the shape of a rectangular environment. Cheng (1986) also proposed an account for how this might take place, an account that has been elaborated by Gallistel (1990). They suggested that animals formed a global representation of the environment, one which was based only on the broad shape of the environment and not on feature information such as corner panels.

The global representation was the principal tool used by animals to find the goal. Rotational errors arose because rats used a record of the environment to find the goal which did not include the source of information which could potentially be used to differentiate the correct location from the rotational error (i.e. the feature information). In many other shapes, such a record would be adequate for unambiguously defining the goal; many shapes do not have rotational symmetry, particularly those which a rat might encounter in the wild. In the rectangle, however, the symmetry of this shape means that the representation of the environment stored in memory may be matched to the real world in one of two ways. One of these is correct, while the other is a 180 ° mismatch - which will lead to a rotational error. This idea is neatly illustrated by the following quote, discussing the results of Cheng (1984):

> The reader may have had the experience of emerging from a subway station or movie theatre in a grid city like Manhattan 180 ° misoriented. One walks with this unwitting misorientation until one fails to find some expected building or street at the spot one takes oneself to have arrived at. There follows a hard-to-describe sense of something rotating inside one's head to produce the proper alignment between the perceived city and one's [representation]. It is conceivable that the same thing happens to the rat when it fails to find the eighteen-pellets on trials when it inadvertently chooses the six-pellet arm first because it is misoriented with respect to the rectangle by 180 °. (Gallistel, 1990, p.193).

Both Cheng (1986) and Gallistel (1990; see also Cheng & Gallistel, 2005) suggest that such a representation is formed by a distinct module called the metric frame, and more commonly referred to throughout the literature as a geometric module. According to Gallistel's conception of a geometric module, it encodes all metric information, both global and local; he also states, however, that it is the global information only which is used to orient in a rectangular environment.

A similar interpretation is offered to account for the results presented by Margules and Gallistel (1988). Rats were trained in a rectangular chamber with feature panels in the corners. In most of their experiments, extramaze cues were available to the rats; in one stage, however, the extramaze cues were obscured, the arena rotated, and the rats disoriented. Without access to extramaze cues, rats were required to use only information provided by the arena's shape, together with intramaze cues, in a situation similar to that used by Cheng (1986). Like Cheng, Margules and Gallistel found that rats chose the two geometrically correct corners more frequently than the others, but failed to distinguish between the correct corner and the corner diametrically opposite – despite the presence of disambiguating feature cues. This pattern of results indicates the use of information provided by the shape of the arena.

Orientation in a rectangular arena by reference to information provided by the shape of the environment has also been observed in a variety of species other than rats. Vallortigara, Zanforlin, and Pasti (1990) trained young chickens to find food buried in a rectangular arena similar to that used by Cheng (1986). In an initial test, the chicks were trained in a featureless rectangle with food hidden in one corner only. In this case, the correct corner could not be distinguished from the opposite corner because the only source of information present was the ambiguous information provided by the environment's shape. Accordingly, the chicks did not show any preference for the correct corner over its rotational equivalent. They did, however, visit these two corners more frequently than the remaining two. The chicks quickly learned to search almost exclusively in either the correct or the opposite corner, demonstrating that, like rats, they were able to use the shape of the environment to orient. In the next experiment, chicks were trained in the same manner except that distinctive feature panels were placed into the corners of the arena. Throughout training, the chicks demonstrated their ability to use these features by selecting the correct corner first on virtually every trial. Not enough errors were made during training to assess the presence of rotational errors and therefore the use of shape; during a test trial, however, the panels were removed and the chicks divided their choices between the correct and the opposite corner. Although they used feature information when available during training, they also learned about the position of the goal according to the information provided by shape.

One way in which the chicks differed from the performance seen in rats was the way in which they responded when the feature and shape information was put into conflict. On a transformation test with the panels moved into new positions with respect to the shape of the environment, rats in Cheng's (1984) study performed at chance levels. The chicks in Vallortigara et al.'s (1990) study performed differently, showing a large preference for searching near to the correct stimulus panel (now in a geometrically incorrect location). This finding perhaps indicates a dominance of feature information over geometric information in these chicks which was not apparent in the rat. The reason for this is unclear; it possibly reflects a cross-species difference in the relative importance of feature and geometric information, or could be a result of the particular feature cues used in the two studies. Perhaps the salience of the features used by Vallortigara et al. was greater than those used by Cheng, such that Vallortigara et al.'s chicks learned more about features in relation to geometric information than Cheng's rats. Regardless, it is clear that chicks, like rats before them, were able to learn about the shape of a rectangular environment and did so even when it was not required for the successful completion of the task. Vallortigara et al. explain these results by suggesting that the processes responsible are similar to those described in rats by Cheng (1986); they conclude that chicks' behaviour is a result of the use of a geometric module for encoding the shape of the environment.

Another species that has been trained and tested in a rectangular arena is the pigeon. Kelly, Spetch, and Heth (1998) trained pigeons to dig for food at one corner of a rectangular maze, with distinctive feature information present in the corners. After training, the birds were given test trials. Those trained with features in the corners were tested either with those features still available, or with the features removed. During the former test trial, the pigeons searched exclusively in the correct corner, demonstrating control of search behaviour by the distinctive cue located there. With no features present, they searched far more often in the two geometrically correct corners than in the two geometrically incorrect corners. Even in the presence of feature information, therefore, they learned readily about the relationship between the goal and the walls of the rectangle. Like Cheng (1986) and Vallortigara et al. (1990), Kelly et al. attribute this behaviour to the encoding of the shape of the environment.

The use of environmental shape as also been observed in fish. Sovrano, Bisazza, and Vallortigara (2002) trained fish on a reference memory task in which they were required to escape from a rectangular tank by locating doors at the corners of the rectangle. Only certain doors could be pushed open, and these doors acted as the goals. With no feature cues present, fish learned to go straight to the correct corner or the indistinguishable opposite corner.

Rhesus monkeys have been trained on a similar type of task. Gouteux, Thinus-Blanc, and Vauclair (2001) trained the monkeys to find food hidden in one corner of a rectangular room. In several versions of the task, monkeys were allowed to observe food being hidden in bedding in one corner of the room before being removed, disoriented, and replaced into the arena. Monkeys were then allowed to search for the food. In the initial version, no feature information was present and animals had to rely upon shape information to locate the goal. Monkeys searched predominantly at the correct corner and the corner opposite, predictably showing no preference for either one of these two due to the lack of disambiguating features. In two additional versions of the task, monkeys were trained in a similar manner but with one wall having a distinctive colour or pattern. This wall was either adjacent to the corner containing food, or on the opposite side of the room. In either case, monkeys disambiguated the two geometrically correct corners but concentrated errors at the corner opposite the goal. These latter two results indicate that, despite the presence of feature information which could be used to isolate the goal, monkeys still used geometric information.

Gouteux et al. (2001) make the surprising claim that their finding of a combined use of features and geometric information is novel as far as animals are concerned. Even a cursory glance at Cheng's (1986) work reveals this to be untrue, as rats visited the correct corner more often than the opposite corner when trained in a reference memory task. Indeed, even in the working memory version of Cheng's task, there was a numerical difference between the frequencies of visits to these two corners; a difference which Cheng suggests likely reflects a significant preference for the correct corner that the statistics are not sensitive enough to show. Nevertheless, Gouteux et al.'s results extend the generality of the ability to navigate with reference to shape, as well as providing an additional indicator that animals are able to use feature information to disambiguate geometrically equivalent locations.

In this thesis, I will present data obtained by training rats in a watermaze. Although there is a solid body of evidence dealing with the issue of learning based on shape, very little of it has been obtained in a watermaze. In a series of experiments reported by Pearce et al. (2001), rats were trained to find a hidden platform in one corner of a triangular pool. The platform could be found only by referring to the triangular shape of the environment. The animals successfully demonstrated the ability to choose the correct over the incorrect corners; they made more frequent visits to the correct corner than to any other throughout training, and devoted more of their time to searching in that area during a test trial with the platform removed. Hayward, McGregor, Good, and Pearce (2003) obtained similar results both in a triangular and a rectangular pool. In the rectangular arena, a visible landmark was placed into one corner, which also contained a hidden platform. Rats quickly acquired a preference for swimming directly to the corner in which the platform was located. During a subsequent test trial with the platform and the landmark removed from the pool, rats showed a preference for swimming in the two corners which had the same geometric arrangement of walls as the corner which had contained the platform; presumably, the choice of these corners over the remaining two reflects learning about the shape of the environment. From these two experiments, then, we can see that learning based on information provided by the shape of the environment can occur when rats are trained in a watermaze.

The experiments reviewed so far show that a wide range of animals are able to navigate in environments with distinctive shapes. This ability is also evident in humans, both in the case of adults (Hermer & Spelke, 1996) and infants (Wang, Hermer, & Spelke, 1999). There is a widespread belief among studies dealing with both animals and humans that, as Cheng (1986) suggested, the ability of animals and humans to navigate according to information provided by environmental shape reflects the existence of a geometric module for encoding the shape of the environment. This belief is illustrated by the following quotations:

> "It seems that chicks (as well as rats) can use...a metric frame (see Cheng, 1986) for encoding the position of the target with respect to the geometric arrangement of the test surfaces" (Vallortigara, Zanforlin, & Pasti, 1990, p. 252-253).
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> "We have shown that pigeons, similar to rats, chicks, and young children encode the geometric shape of the environment" (Kelly, Spetch, & Heth, 1998, p. 268).
>
> "Young children oriented themselves by analysing the shape of the environment. They failed to orient themselves in accord with non-geometric landmarks that could have improved their performance...These findings provide evidence for a common shape-based orientation mechanism in humans and other animals" (Hermer & Spelke, 1994, p. 58-59).
>
> "By testing nonhuman primates in a task similar to that used by Cheng (1986) and Hermer and Spelke (1996) we provide further evidence of a common orientation mechanism, which is based on the geometry of the environment...it seems there is a unit in the mammalian brain that specifically encodes the geometric properties of the environment" (Gouteux, Thinus-Blanc, & Vauclair, 2001, p. 516).
>
> "These findings [with fish], together with those obtained from birds...and mammals...suggest that the ability to use purely geometric information for reorientation is widespread among vertebrates, likely representing an evolutionarily ancient trait and a very basic cognitive mechanism" (Sovrano, Bisazza, & Vallortigara, 2002, p. 56-57).

Despite this common conclusion, it is my belief that the existence of a global representation has not yet been proven. Alternative explanations are available for the results of the studies summarised so far, and the proposal by Cheng (1986) that animals possess a geometric module has not been subject to proper critical evaluation. Although there is ample evidence that animals are able to orient with respect to information provided by the shape of the environment, this need not be as a result of animals using global cues. Local information provided by shape is also present which adequately explains these results. By way of example, suppose that the hidden goal is located in corner A of the rectangle shown in Figure 1. Although it is possible for learning about the goal to progress according to global cues, it is also plausible that animals may learn about the position of the goal in relation to some relevant local cue, a part of the shape such as wall AB. The location of the platform is constant in relation not only to the overall shape of the environment, but also to single features of the shape. It would be sufficient, then, to learn the position of the goal in relation to any such shape feature. The experiments summarised so far are consistent with both these types of account, and we are not able to draw any conclusions from this evidence about the likelihood of orientation progressing according to global or local information.

Two studies have attempted to provide an answer to this question, using a transformational approach. Animals were trained in an environment with a distinctive shape, before being tested in a transformation of that space. In both experiments, the new arena preserved some local features while altering the broad environmental shape. If animals learned to use the overall shape of the initial environment, then they should show little transfer to the new space. Alternatively, a strategy based upon local cues should result in those animals showing a preference when placed into the new arena which is consistent with the ongoing presence of those local cues.

The first such experiment was reported by Tommasi and Polli (2004), who trained chicks in a parallelogram-shaped enclosure. A parallelogram is composed of two long walls and two short walls in the same way as a rectangle, but has two acute-angled corners and two obtuse-angled corners. Corners of the same angle are located opposite one another. When trained to find food hidden in one corner of this arena, chicks quickly learned to go to either the corner containing the food or the opposite, identical corner. Several test trials were then conducted, with the aim of assessing the use of two types of local cue. In the first test, designed to test the chicks' use of information concerning wall length, the birds were placed into a rectangular arena. This arena had the same length walls as the parallelogram, but all four corners were right-angled. The overall shape of the environment, therefore, was different – but the local information provided by the lengths of the walls was preserved. On this test trial, chicks searched predominantly in the two corners which had the same arrangement of wall lengths as the correct corner in the parallelogram. The second test was designed to assess the use of local information provided by the angles subtended by the wall at corners. Chicks were placed into a rhombus-shaped arena; this was composed of four walls of the same length, but the angles at the corners were the same as the angles at the corners in the parallelogram. On this test trial, chicks searched mainly in the corners of the rhombus which had the same angle as the correct corner in the parallelogram.

In both tests, chicks showed behaviour which was consistent with the use of local cues but inconsistent with the notion that they relied primarily on global cues for orientation in the parallelogram-shaped enclosure. The second set of experiments in which the use of local cues was assessed using a transformed arena was reported by Pearce, Good, Jones, and McGregor (2004). Rats were trained to find a hidden platform in one corner of a rectangular watermaze, in a similar manner to Hayward et al. (2003). Following this training, rats were transferred to a 'kite-shaped' arena. This shape was composed of the same four walls as the rectangle, but in a different arrangement. Two of the corners of the kite were right-angled, each composed of one long wall and one short wall. Each of these right-angled corners was the mirror image of the other. When transferred into this shape, rats were trained with the platform located at either the corner which had the same arrangement of walls as the correct corner in the rectangle (the congruent group), or the corner with the alternative arrangement (the incongruent group). During training in the kite-shaped pool the congruent group visited the platform containing the corner more frequently than the incongruent group, suggesting that both groups of animals had learned the position of the platform in relation to local information in the rectangle. In a second experiment, rats were trained initially in the kite-shaped pool before being transferred into the rectangle. The results were similar to those obtained from the first experiment, with a congruent group visiting the corner containing the platform far more frequently than an incongruent group.

The findings of both Tommasi and Polli (2004) and Pearce et al. (2004) suggest that animals are able to navigate in an environment with a distinctive shape by reference to local cues. The transfer shown between environments with different shapes is not compatible with the idea that animals orient in such situations according solely to global information. As such, the available evidence gives little support to the idea that animals learn about the macroscopic shape of their environments.

Shapes created by groups of landmarks.

The evidence reviewed so far concerned learning about solid-walled shapes. As I have summarised, there is little conclusive evidence that animals learn about shape under these conditions. An additional matter of interest is whether animals learn about shape when it is provided not by surfaces, but by discrete landmarks. In this section, I will review several experiments designed to examine animals' use of shape when that shape is defined by the spatial relationships between landmarks. Many of the results presented here are consistent with the idea that animals encode the overall shape created by the landmarks; but, as in the previous section, these findings can be explained by assuming that spatial learning is based on local cues.

Relatively little research has examined the extent to which animals are able to use the shape of an array of discrete intra-maze landmarks to locate a hidden goal. In a thought-provoking and highly influential series of experiments, Collett, Cartwright, and Smith (1986) trained gerbils to find hidden food by using various arrangements of landmarks. This was done in full view of room cues, which provided additional directional information. As a result, gerbils demonstrated the ability to search at a particular distance and direction from a single symmetrical landmark, even when that landmark was moved into a new position in the room. Since a single symmetrical landmark is incapable of providing the necessary directional information to do this, the gerbils must have paid attention to the room cues.

In some of Collett et al.'s (1986) experiments, a group of three distinctive landmarks was shown to gain control over search behaviour. Animals were trained with a triangular array of landmarks, with food hidden outside this triangle. Animals quickly learned to search at the location at which food was hidden. When the array of landmarks was rotated, gerbils searched chiefly at the location which preserved the original relations of the food to the shape of the three landmarks. This behaviour could occur as a result of learning based on all three landmarks, but could also be based on local properties of the array such as any one of the constituent landmarks. This learning could progress in the same way as previously demonstrated with a single landmark. I am unable to confirm which of these strategies was used.

Evidence for the use of local cues is provided by the results of an experiment in which gerbils were trained to find food in the centre of a triangular array of landmarks. Following acquisition, the array was rotated through 60 ° and animals were allowed to forage for food. In addition to searching in the centre of the array, the gerbils searched in areas outside the triangle formed by the landmarks. These positions preserved the distance and direction of the goal from individual landmarks, suggesting that the animals had leaned about local cues.

Further evidence for the use of local information is provided by an experiment in which gerbils were trained to locate food hidden at a fixed distance and direction from a pair of distinctive landmarks. After acquisition, they were tested with the landmarks separated by an increased distance. Animals now searched in two discrete locations, one at the correct distance and direction from each of the two landmarks. This suggests that, in the previous training phase, the gerbils learned a separate bearing for finding the goal based on each of the landmarks. If they had learned to find food based on a global representation, they should have either shown no preference for searching in any area around the transformed array or searched at a single location consistent with the expansion of the shape. Rather, they had learned to find the goal by use of local cues. It is inconsistent with the idea that animals rely solely on a global representation to find the goal in the training stage, although the possibility remains that both a global and a local strategy were learned during acquisition. Collett et al.'s (1986) experiments cannot confirm this. Conversely, they do show that animals can learn spatial relationships based on local cues.

A different result has been obtained using Clark's nutcrackers (Kamil & Jones, 2000; Jones & Kamil, 2001). The position of a hidden goal was defined by two differing landmarks, with the goal located at a constant bearing from each; the two landmarks and the goal were located at the vertices of an isosceles triangle which always had the same angles. The size of this array was, however, varied throughout training. One result of this manipulation was that the distance from each landmark to the goal was not constant; despite this, birds quickly learned to search for food in the correct location. This procedure differs from that used by Collett et al. (1986) in that Collett et al.'s gerbils were able to use either one or both landmarks to find the hidden goal, whereas the only consistent strategy available to birds trained with a variably-sized array is to use both landmarks. This does not, however equate to the use of global information provided by the array. It is equally plausible that distance-independent bearings from each landmark to the goal were formed, and that the birds learned to search for food at the intersection of these two bearings.

Another study attempting to show that animals can learn about the spatial arrangement of an array of landmarks was reported by Greene and Cook (1997). Rats were trained to find food baits hidden in a circular arena which contained 24 uniformly distributed vertical poles. The food was hidden on top of six of these columns, and could be found by searching at the top of the correct poles. The identity of the baited poles was defined by the locations of a set of six distinctive landmarks placed within the arena. After training, rats were tested with a number of transformations of the original space. In one set of test trials, the six familiar landmarks were used. They were positioned either in the same configuration as they were during training, in a novel arrangement which used the same six locations but with the landmarks swapped around into positions they had not previously occupied, or with six novel locations in the arena. Performance was best when the animals were tested in the original training conditions, but the ability of the animals to search in the correct locations in relation to the shape of the landmark array was greater during the test trial with the exchanged positions than during the test with novel locations. This pattern of results was mirrored when a novel set of landmarks was used, either when these were six new distinctive landmarks or when all six were identical.

Greene and Cook (1997) state that this latter result demonstrates encoding of the spatial relationships between the set of landmarks, and conclude that rats may form a global representation of their environment. What does seem fairly certain from the differential performance of rats when presented with novel landmarks in either familiar or novel arrangements is that they are sensitive to at least some aspect of the way in which the landmarks are arranged. However, their results can also be explained by assuming that the rats learned to find the food baits based on local cues provided by the arrangement of the landmarks. By way of example, suppose that each animal has learned about a group of landmarks which are positioned in close proximity to each other. In the diagrams of the training apparatus provided by Greene and Cook (p. 320, Figure 4.), there is a cluster of three landmarks close together near to the periphery of the arena. The site of this landmark cluster is sufficient to provide orienting information to the animals, and to define the locations of the goals. The identity of the landmarks is not important for the success of this strategy; merely that a cluster of three landmarks in close proximity can be located. In test trials with a novel configuration of landmarks, no such group may be present and the usefulness of the strategy would be drastically reduced. Hence, it is possible for animals to be sensitive to changes in the spatial configuration of landmarks without learning their relative positions in the arena.

Benhamou and Poucet (1998) trained rats to locate a hidden platform in the watermaze by referring to a set of three discrete and distinctive landmarks. These experiments were designed to assess animals' use of the overall configuration of the landmarks to locate the platform. In the first experiment, rats were trained with one of two triangular landmark configurations. In the isosceles condition, the landmarks were arranged in an isosceles triangle in one half of the pool, with the platform located in the half of the pool which did not contain any landmarks. In the equilateral condition, the landmarks were spaced evenly around the pool so that they formed an equilateral triangle, and the platform was located between two of the landmarks. In this condition, the geometric properties of the landmark array were ambiguous; the shape created by the landmarks had three axes of symmetry and therefore defined three equivalent possible locations for the platform. In order to disambiguate these locations, the identities of the landmarks had to be used. In the isosceles condition, however, the location of the platform was unambiguously defined both by the identities of the landmarks and by the configuration of the array. In this condition, test trials with the platform removed revealed a strong tendency for rats to search in the correct area of the pool. In the equilateral condition, however, rats failed to disambiguate the correct location from the two alternative places which had the same relationship to the shape created by the array. Benhamou and Poucet argued that this pattern of results indicates a tendency for rats to use shape information to find the platform, in preference to feature information. The results of the equilateral group, they claim, show that this was the case even when the spatial arrangement of the landmarks is insufficient to accurately complete the task.

One difficulty in accepting their analysis is that the data presented in this article are not complete. For the equilateral group, no data are presented relating to time spent searching for the platform in areas other than the three locations specified by the shape of the landmark array. With this is mind, we cannot be sure if these rats are using the configuration of the landmarks at all; the typical swim path provided by the authors suggests that the animal in question may have simply swum between the three landmarks, rather than the possible goal locations defined by them. Although swimming from each landmark to the next would necessarily take an animal through the potential goal locations, this does not give us any indication of whether or not the rats actually searched in these areas. If they swam more slowly here, or spent more time searching at these points on the path, we might be able to conclude that they expected to find the platform in one of these three areas. Without such additional data, we cannot confirm this idea. As such, the configuration of the landmarks may plausibly have been ignored by the animals in favour of a simple strategy of swimming from one landmark to the next, which would lead them to discover the platform readily.

For the isosceles group, we are equally unable to assess their use of shape because the platform may simply have been found by searching in the half of the pool that did not contain any landmarks. The authors acknowledge this latter problem, and attempt to address it by presenting a second experiment conducted with landmarks again arranged in an isosceles triangle. In this experiment, the platform was located either in the east or the west half of the empty portion of the pool. In test trials with the platform removed, rats showed a preference for swimming in the correct rather than the incorrect side of the area containing no landmarks, a result which would not be possible if rats simply learned to swim in the empty half of the pool. It does not, however, require a drastic modification of the strategy to enable it to solve this task. All that is needed is some additional directional component, a left/right preference that, when combined with the tendency to swim away from the landmarks, produces some command such as 'swim away from the landmarks and to the left/right'. Once again, no representation of the shape created by the landmarks is needed to succeed on this task.

These experiments, then, provide little evidence that animals encode the positions of all landmarks within their environment and organise them into a global representation. Findings from both gerbils (Collett et al., 1986) and rats (Greene & Cook, 1997; Benhamou and Poucet, 1998) can be explained by appealing to simple strategies based on local rather than global features. Two experiments have been reported which demonstrate more forcefully the use of local cues when shape is provided by an array of landmarks. Spetch et al. (1997) trained pigeons to find food hidden at the centre of a square created by four discrete landmarks. Following this training, the shape was expanded and the birds allowed to search for the food in this larger square. If they used the overall shape of the array to find the food, the pigeons should have searched in the centre of the new shape. Typically, however, they searched in four locations, each of which was located at the same distance and direction from one landmark as the food had been during the training phase. This finding is most easily explained by supposing that the birds had learned to find the food by reference to individual local cues.

Esber, McGregor, Good, Hayward, and Pearce (2005) trained rats to find a hidden platform in a watermaze. These experiments were based partially on the experiments of Pearce et al. (2004), who trained rats in a rectangular pool before placing them into a kite. Esber et al. trained animals under similar conditions, except that the shapes were created by four identical cylindrical landmarks positioned at the periphery of a circular pool. After being trained to find the platform in one corner of this rectangular array, rats showed a preference for going to the corner in the kite which had the same geometric arrangement as the correct corner in the rectangle. In a similar way to the results obtained by Pearce et al., this is most likely due to learning based on local cues, since the global arrangement of the landmarks changed. An example of a suitable local cue might be a long or a short 'side' of the notional shapes formed by the two landmarks arrays. Also consistent with this idea are the results of a further experiment in which rats were trained to find a platform in one corner of either a rectangular or a kite-shaped array of landmarks, before being tested with some of those landmarks removed. In both cases, rats continued to search in the locations which preserved relations with the remaining landmarks. In the rectangle for instance, two landmarks were removed, leaving a 'short side' of the rectangle. After this transformation, rats searched at the end of this short side which was consistent with the relationship of the platform to the short sides of the rectangle in the previous stage. This shows how orientation based on local cues progresses in an array of landmarks even when other strategies are readily available.

The results of Spetch et al. (1997) and Esber et al. (2005) strongly support the idea that animals are able to find a hidden goal in an array of landmarks by using local cues. While some of the data reviewed in this chapter can be explained by assuming that animals form a global representation of their environment, these findings may also be accounted for by appealing to simpler explanations based on local cues.

I have considered evidence obtained by training animals in shapes made up of walls of their environment, or separate landmarks. Despite the failure to show that animals learn about the global shape of their environment, I have reviewed several experiments which demonstrate the use of local cues. The most parsimonious explanation for these findings is that animals do not use global cues, but rely on local information to navigate. In this thesis I will present evidence from new experiments, with the aim of further assessing animals' use of these two types of information.

The hippocampus.

In this section I will review the findings from a number of studies which suggest that the hippocampus has a role in spatial memory. Historically, there has been a significant interest in the hippocampus as a site for memory processes. This interest began with observations of a human patient, HM, by Scoville and Milner (1957). HM had undergone a bilateral temporal resection as an experimental treatment for the epilepsy from which he suffered; the operation was partially successful in relieving his epilepsy but also resulted in a marked global amnesia. Among the structures to which HM sustained damage were the perirhinal cortex, amygdala, and all but a small posterior part of the hippocampus. Despite the fact that HM's lesion extended well beyond the hippocampus, it was the damage to this region which was thought to be responsible for many of the mnemonic deficits from which he subsequently suffered. In fact, later studies of patients with damage more closely restricted to the hippocampus revealed less severe memory deficits than those seen in HM (Squire, Amaral, & Press, 1990). This might lead us to conclude that not all of the memory processes affected by HM's lesions were dependent upon the hippocampus; nevertheless, Scoville and Milner's observations represent a starting point for the ongoing debate over the mnemonic function of the hippocampus.

In animals, a common method of investigation has been to observe behaviour following administration of lesions to the hippocampus. This method has produced a wealth of information concerning the effects of hippocampal damage. Of particular relevance to this thesis are those studies which have attempted to assess the ability of animals with hippocampal damage to perform spatial tasks. One early attempt to do this was reported by Kimble (1963), who compared the performance of rats with hippocampal damage to controls on a maze task. This work was based partially on the observation by Dashiell (1930) that rats are able to acquire a 'sense of direction', which specifies the direction in which they need to move in order to reach a goal from a given start point. Dashiell trained rats to navigate to a goal in a large rectangular maze with partitions placed into the arena in order to obscure the shortest possible path. The positions of these partitions were changed between trials so that the necessary route was different each time, but the overall direction from the start to the goal was constant. When trained in this manner, rats became increasingly likely to enter blind alleys when they pointed towards the goal rather than away from it. Such a preference suggests that the animals were sensitive to the overall bearing to the goal. Kimble trained both hippocampectomized and control rats on a version of this task, and once again found a tendency for controls to make increased errors in blind alleys which pointed towards the goal. Operated animals, however, failed to show this characteristic error pattern. Comparing two critical trials, one with a maze configuration which could be solved simply by moving from the start towards the goal and one which required a turn away from the goal, control rats made around three times as many errors on the convoluted maze than the simple maze but lesioned animals had an equivalent error rate in each. Kimble suggested that the lesioned animals were not, as the control rats were, influenced by a sense of direction.

More recent research into the effects of hippocampal lesions on spatial behaviour has focussed on tasks which involve the use of an array of either proximal or distal landmarks. A good example of a procedure which utilises distal landmarks is the radial arm maze, an appetitively-rewarded task in which animals are required to run down particular arms of the maze in order to obtain food rewards hidden at the arm ends. In a simple version, the maze may have eight arms radiating from the centre and food hidden at the end of each one. The optimal strategy for retrieving all food baits is to run down each arm once, making a total of eight arm entries and visiting no arm more than once. Any repeat entries to the same arm are errors, and are unrewarded because those arms are no longer baited with food. This version of the radial arm maze was used by Jarrard (1978), who compared the performance of rats with hippocampal lesions with controls. Performance was measured by recording the number of correct arm entries made in the first eight choices; a perfect performance, visiting each arm once and making no errors, would result in a score of eight. Unoperated controls and rats subjected to a control operation performed well on this task, with the average score during the second half of training exceeding seven out of eight choices correct. Rats with total lesions of the hippocampus were significantly impaired, scoring an average of around 5.6 choices correct out of every eight. Lesioned rats performed more poorly either when the task was learned postoperatively, or when lesions were administered after some training had taken place.

Becker, Walker, and Olton (1980) trained rats with a variety of different lesions to perform the same radial maze task. While rats with lesions to the fimbria fornix (which provides the hippocampus with a substantial part of its afferent connections) never exceeded the level of performance expected by chance, those with lesions of the amygdala or caudate nucleus performed as effectively as both operated and unoperated controls. A further elaboration of this finding was provided by Olton, Walker, and Gage (1978), who demonstrated a profound effect of lesions designed to disconnect the hippocampus from neighbouring areas when those lesions were administered after training; this finding indicates that the hippocampus is not only required for acquisition of a spatial task, but also for subsequent performance.

Another spatial task affected by lesions of the hippocampus is the spatial alternation task (Aggleton, Hunt, & Rawlins, 1986). Rats were tested in a T-maze, which consisted of three arms arranged in a 'T' shape. Rats were placed onto the lower arm, and allowed to run along this arm to the junction of the maze. For a sample trial, one of the top arms was blocked, forcing rats to choose the other arm. The available arm was baited with food in a small well at its end. After consumption of this food, rats were removed from the maze and a test trial occurred. On this trial, both of the top arms were available for selection but only the previously blocked arm was baited. If a rats entered the arm which it had already visited, the junction of the maze was blocked and the rat was removed shortly afterwards. These trials were not rewarded. In order to obtain reward, therefore, a rat had to run down the arm it had not previously visited; in other words, it had to alternate choices between the left- and right-hand arms. Aggleton et al. demonstrated that rats with hippocampal lesions were not able to learn this task, and did not exceed chance performance. In stark contrast, both sham rats and cortical controls quickly learned to alternate their choices in order to obtain reward.

A different technique for assessment of the use of spatial information is based on the object recognition task. This task was devised by Ennaceur and Delacour (1988), who used the natural tendency of rats to explore novel cues to assess their ability to recognise objects. Two objects were placed within an open field, and rats were allowed to explore these objects for two minutes. In a subsequent test trial, animals were once more placed into an arena with two objects, one of which had been present on the previous trial. The other object was novel; typically, on this test trial, rats spent more time exploring the novel than the familiar object. This, Ennaceur and Delacour reasoned, was due the ability of the rats to recognise the familiar object and to therefore treat it as being familiar. Mumby, Gaskin, Glenn, Schramek, and Lehmann (2002) tested rats in several different versions of this task, with the aim of examining several different types of novelty. In the basic version, they replicated earlier results and showed that rats had a preference for exploring novel rather than familiar objects. In a 'place familiarity' version, the same two objects were presented during the exposure and test trials but one of these objects was moved to a novel location prior to test. In this case, during the test trial both objects were familiar but they were in one familiar location and one novel location. Mumby et al. found that rats had a strong preference for exploring the object which was in a novel location. In another version, animals were allowed to explore two objects separately, each in a different context. On a test trial, the two objects were presented together in one of the two exposure contexts. One of the objects was in a familiar context, while the other was in a novel context; on this test trial, rats spent more time exploring the object which was in the novel context. In this way, they were sensitive to the context in which an object occurred. Of particular interest here are the findings from additional groups of rats with hippocampal lesions, tested on each of the tasks just described. These rats adequately demonstrated a preference for a novel over a familiar object in the object recognition task, but did not show a preference for novelty in either the place task or the context task. Such a finding is consistent with the idea that the hippocampus is important for remembering contexts and places.

The hippocampus is also implicated in place recognition work carried out by Hollup, Kjelstrup, Hoff, Moser, and Moser (2001). Rats were trained in an annular watermaze, a circular track-shaped pool with a remotely controlled escape platform. The platform was unavailable at first, so that rats were forced swim around the annulus of the pool. After at least one full circuit, the platform was made available.

Rats quickly learned to climb onto this platform, the location of which remained constant throughout training. On a test trial, the platform was not present. If rats recognised the goal location, they should have swum more slowly in the area of the goal in order to facilitate search behaviour. Rats with hippocampal lesions and control rats were tested on this task, and the results supported the idea that the hippocampus is required for the recognition of places; while control rats swam more slowly in the area which had contained the platform than in others, the lesioned rats did not. Hippocampal rats presumably did not recognise the platform's former location. This finding is entirely consistent with the results reported by Mumby et al. (2002), and reinforces the idea that the hippocampus is required for place recognition.

When rats are placed into a circular watermaze with visible extramaze cues, they are quickly able to learn to swim to and climb onto a submerged platform provided its location is consistent from trial to trial (Morris, 1981). Rats learned this task even when their start point was varied between trials, eliminating the possibility that the animals simply learned to swim in a particular direction from the outset. Location of the platform is likely, therefore, to be dependent upon the use of distal cues to learn the place in the pool at which the platform is positioned. In a further experiment (Morris, Garrud, Rawlins, & O'Keefe, 1982), rats with hippocampal lesions were trained on this task alongside controls. While the control animals learned to find the platform with ease, those with hippocampal lesions did not. They took longer to find the platform than controls, and the paths they took to reach the platform were markedly less direct. In addition, in a test trial with the platform removed, lesioned rats spent less time searching in the region surrounding the platform's former location than control animals. One possible explanation of these results is that the lesioned animals were poorer on some theoretically uninteresting dimension such as motor ability; to test this, a second phase was conducted during which the platform was just visible above the surface of the water. The platform could now be located simply by use of a homing strategy. In this phase, all animals (including those with hippocampal lesions) learned to swim quickly to the platform. There was no difference between the performance of the lesioned and control animals. In a test phase with the platform removed, however, the lesioned animals did not show a preference for swimming in the area in which the platform had been located. Without a local visual cue, lesioned rats were not able to find the platform. Although they had been able to find the visible platform easily, no spatial learning had occurred as a result of this training.

These studies demonstrate that, following hippocampal lesions, rats show a deficit on a wide range of spatial tasks. Deficits in spatial learning have also been observed after saturation of long-term potentiation (LTP) in the hippocampus (e.g. McNaughton, Barnes, Rao, Baldwin, & Rasmussen, 1986). LTP (Bliss & Lomo, 1973) is the putative mechanism by which synaptic changes supporting learning may occur. If LTP is saturated by electrical stimulation, further learning should not be possible. Moser, Krobert, Moser, and Morris (1998) induced saturation of LTP in the hippocampi of rats before testing them on a behavioural watermaze task. Those rats with saturated LTP performed at chance on this task, whereas rats subjected to electrical stimulation but still capable of further potentiation showed undisrupted performance compared to controls. These results suggest that for performance of such spatial tasks, the hippocampus must be not only present, but capable of supporting further learning. It is worth mentioning the ongoing debate over the role of LTP in learning when considering these results (for a full discussion, see Shors & Matzel, 1997), but they are at the very least consistent with the notion that the hippocampus is required for spatial learning.

Neurophysiological evidence also supports the idea that the hippocampus is involved in spatial learning. O'Keefe and Dostrovsky (1971) recorded activity in cells of the dorsal hippocampus and dentate gyrus in rats, and attempted to correlate the firing patterns of these cells with aspects of the rats' behaviour. Some cells within these regions showed firing patterns closely related to the region of space occupied by the animal, and were termed 'place cells'. Place cells are those which fire maximally when an animal occupies a particular region of space, which is commonly referred to as the place field of the cell. In any other region the cell fires infrequently; when the animal is located within the cell's place field, the firing rate of that cell increases dramatically. This increase in firing is not associated with any aspect of the animal's behaviour, merely its occupation of the place field. Since each cell has a distinct place field, it is claimed that each codes for a particular place.

If we are to believe that these cells code for particular places, then we might expect that they would be sensitive to the kind of cues by which places are commonly identified by animals. The main source of information that studies of spatial learning in rats has focussed on has been visual information. Accordingly, place cells have been shown to alter their place fields when changes are made to the visual cues available for orientation. O'Keefe and Conway (1978) recorded from cells in the hippocampus while animals explored a maze in full view of extramaze cues. Once they had found place cells and recorded for each one exactly where the place field was located, they moved the extramaze cues. More specifically, they rotated these cues around the maze. Following this manipulation, the place fields of the cells altered – they moved in tandem with the cues, so that the place field of each cell maintained a constant relationship with the cues outside the maze. Another way of assessing the control extramaze cues exert over place cell firing is to rotate the maze within the external environment. Olton, Branch, and Best (1978) trained rats in a radial maze with extramaze cues available before rotating the maze within the room. The place fields of the cells remained consistent with the room, rather than with respect to any particular arm of the maze.

Distal cues are not the only source of information that can influence the place fields of place cells. Shapiro, Tanila, and Eichenbaum (1997) trained rats in a radial maze with distinctive intramaze tactile and visual information, before altering both the orientation of the maze and the positions of extramaze cues. Each was rotated through 90 °, in opposite directions so that the relative rotation of the maze to the room cues was 180 °. Some of the cells altered their firing patterns to be consistent with the room cues, and some remained consistent with the proximal maze cues. They demonstrated, then, that both distal and proximal information can influence the firing patterns of place cells. There is, however, little evidence concerning place cells and proximal cues. This possibly reflects the greater reliability of distal cues in natural settings to provide the directional information necessary to determine a place. In any case, the place fields of these cells certainly seem to be governed by both distal and proximal cues under some circumstances; sensitivity to both kinds of visual cue lends credibility to any claim that place cells are an integral part of the navigation system in animals.

We have compelling evidence that the hippocampus is involved in navigation; we are less certain, however, of what its exact role is. A popular account was proposed by O'Keefe and Nadel (1978). Their influential book, *The Hippocampus as a Cognitive Map*, contained a detailed account of a number of different types of navigation. By linking the presence of place cells within the dorsal hippocampus with the results of studies assessing the spatial abilities of animals with hippocampal lesions, they concluded that animals possess a map located within the hippocampus, and that the use of this map is one of the primary strategies used by animals to navigate. In fact, O'Keefe and Nadel were not the first to suggest that animals store spatial information in the form of a cognitive map. They were preceded by Tolman (1948), who demonstrated that rats were able to take a novel shortcut in a maze; a behaviour which, he argued, could not possibly arise from strategies that were not map-like in nature. Rather, Tolman suggested that it was a result of animals' possession of a representation of space which encompassed the relations between all objects – even those which had not previously been experienced together. This representation would then allow the animal to compute a novel route. Tolman called this representation of space a cognitive map, but the concept remained relatively undeveloped until O'Keefe and Nadel published their book (for a fuller discussion of this and other evidence relating to cognitive maps, see Mackintosh, 2002).

O'Keefe and Nadel (1978) proposed two separate navigational systems. The first, called the *taxon* system, is an associative mechanism analogous to the learning of routes. Learning by this method would take the form of associating each point on a route with the next via responses – movements between the series of places which comprise the route. This is an inflexible strategy, and only allows navigation along the route without deviation. This method of navigation is, they claim, independent of the hippocampus. Alternatively, the *locale* system takes the form of a map, a global representation which encodes the position of every experienced location within a given environment. Since the position of each landmark is encoded in relation to every other, an animal possessing such a representation would not need to have previously taken a path between any two given points in order to be able to make the journey from one to the other. This representation, then, leads to a much advanced level of flexibility when compared to a taxon strategy. According to O'Keefe and Nadel, the locale system is based within the hippocampus.

A cognitive map is a type of global representation, much like the geometric module proposed by Cheng (1986). Cheng considers the possibility that the two are the same, with the proviso that the geometric module is a map which encodes locations primarily by their relation to shape. Following my review of shape learning experiments, I concluded that there was not enough evidence to conclude that animals possess a geometric module. Similarly, the evidence for a hippocampal-dependent global representation such as a cognitive map is less than convincing.

Although it is not difficult to understand how place cells could be involved in a cognitive map, it is also possible that they are involved in processing local cues. For an animal to know where it must go in order to reach a destination, it must first calculate its current position. The activity of place cells is inextricably linked with current position and may be accordingly useful in working out the appropriate path to take. Such a role for place cells fits just as easily with a system based on local cues as it does with a global representation. The difficulty in distinguishing between the two types of account is that placing an animal in a location and observing increased firing in a cell does not tell the experimenter anything about how exactly the animal represents that particular place. If we assume that the animal is recording its position in allocentric space, we might conclude that the cells are the basis of a cognitive map. If, however, this location is encoded simply in relation to some other landmark(s), it might merely be a place representation – and not part of a map. Support for this latter possibility comes from Hetherington and Shapiro (1997), who recorded activity in place cells while rats explored a square chamber. Distinctive cue cards were attached to three of the four walls; when any single card was removed, the activity of place cells altered. The firing rates of cells with place fields close to the removed cue's former location were reduced, while cells with distal place fields increased. What this result demonstrates is that each place cell behaved differently when a cue near to its place field was removed than when the altered cue was further away. This dissociation between the effects of removing cues close to and far away from a cell's place field suggests that place cells are sensitive to local cue information, rather than all cues within a given environment. This local bias is most consistent with the idea that cells in the hippocampus represent places without putting them into a global representation.

The deficits observed in spatial tasks are also easily explained by assuming animals with hippocampal lesions were impaired in their use of local cues. In several of these experiments, rats with hippocampal lesions performed more poorly than controls at identifying a location (Mumby et al., 2002; Hollup et al., 2001; Morris, 1982). In each case, it is equally plausible that the place in question was defined by controls according to global and local cues. Although it has been traditionally assumed that a global representation is used to find the platform, learning based on a single extramaze cue near to the area containing the platform would be capable of producing a preference for the correct area of the pool. If controls used local cues, then we would conclude that the hippocampus is critical for encoding this type of information. Results obtained in a radial arm maze are also easily accounted for by appealing to an explanation based on local cues. Olton (1978) suggests that his own results may have arisen from rats learning about each arm of the maze as an isolated stimulus, rather than encoding the spatial relationships between them.

The problem with attributing spatial deficits following hippocampal lesions to the loss of a global representation is that little evidence exists to suggest that the control groups in these experiments used global cues. A more satisfactory method of testing the notion that the hippocampus is the site of a global representation would be to compare lesioned animals with controls on a task which is demonstrably dependent upon the use of global cues. The type of transformational approach described earlier might be capable of revealing the use of global cues, although the evidence to date suggests that this does not occur. Nevertheless, the simultaneous assessment of performance following hippocampal lesions and the use of global cues is a priority if we are to draw any firm conclusions about the presence of a hippocampal-dependent global representation.

Summary of aims.

In summary, I have reviewed evidence concerning both navigation in environments with distinctive shapes and the role of the hippocampus in spatial tasks. Accordingly, there are two key aims of this thesis.

I will attempt to shed further light on the mechanisms by which animals use information provided by the shape of the environment to locate a hidden goal. Specifically, I will focus on whether global or local information is used. Where there is evidence that animals use local cues, I will attempt to identify them.

The role of the hippocampus in navigation will be further elaborated, with particular emphasis on shape-based learning tasks. This will be achieved primarily by the comparison of performance between rats with hippocampal lesions and sham operated control rats.

CHAPTER TWO

EXPERIMENT 1

Experiment 1 was designed to address both of the principal aims of this thesis: to elaborate our knowledge of the spatial deficit observed after hippocampal lesions, and to determine whether learning to orient according to information provided by the shape of the environment progresses by the use of global or local cues. Specifically, I aimed to provide answers to two questions, which I will deal with in turn.

1. Is the hippocampus necessary for navigation according to the shape of the environment?

As summarised in the introduction, a wide array of spatial deficits have been observed in animals following lesions of the hippocampus. O'Keefe and Nadel (1978) have suggested that this is because the hippocampus is the site of a cognitive map, a type of global representation of the environment. The geometric module proposed by Cheng (1986) and Gallistel (1990) is another type of global representation. It does not seem unreasonable to suggest, then, that damage to the hippocampus should disrupt the use of such shape properties and impair the performance of animals on a shape-reliant navigation task.

Experiment 1 assessed the ability of rats with damage to the hippocampus to locate a hidden platform in a particular corner of a completely white (W) rectangular watermaze (upper panel of Figure 2). A group of hippocampectomized rats (the hippocampal-W group) as well as a group of control animals (the sham-W group)

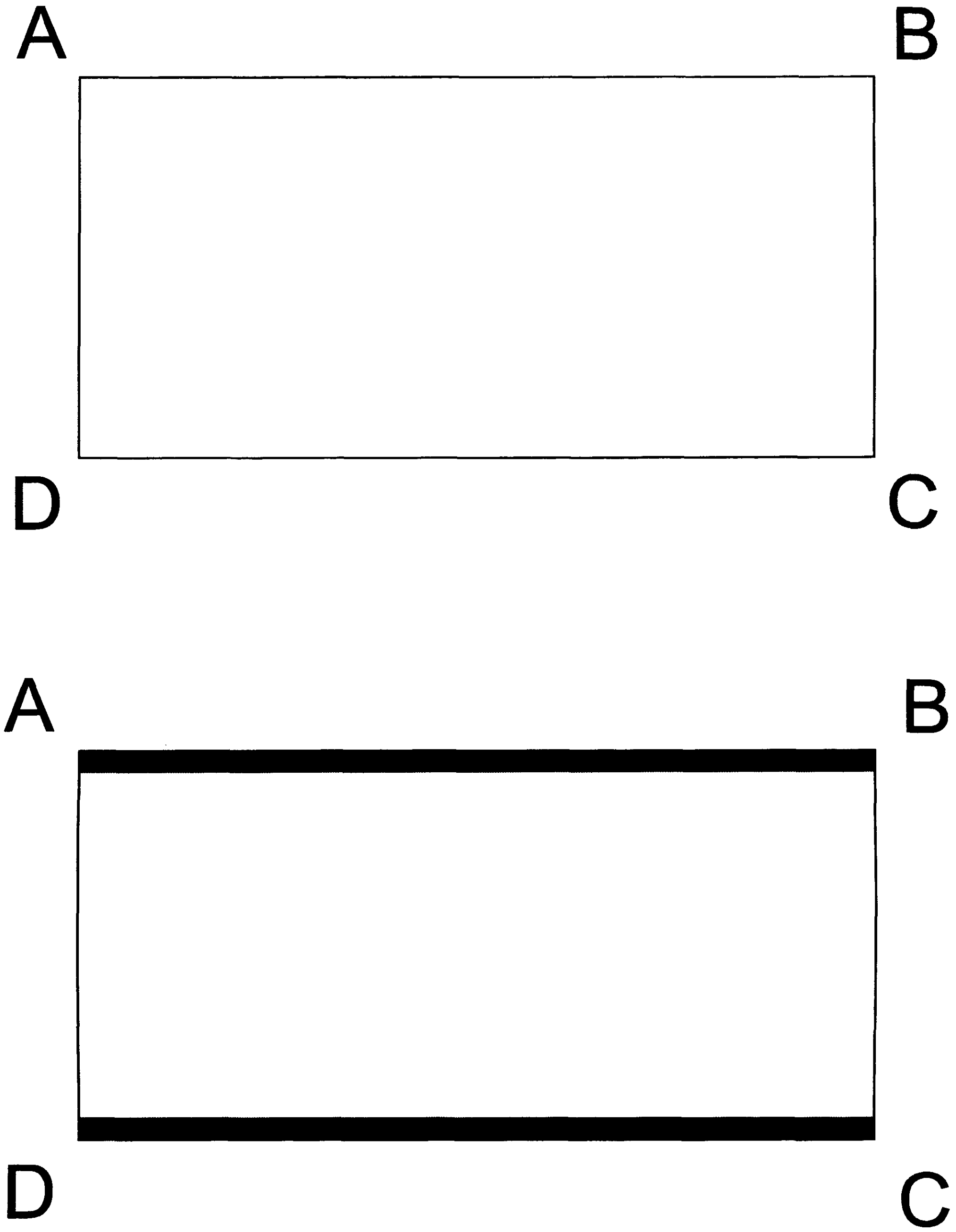

Figure 2. Schematic overhead views of the two test environments in which animals were trained during the rectangle stage of Experiment 1. The hippocampal-W and sham-W groups were trained in a rectangular environment with four white walls (top panel) and the hippocampal-BW and sham-BW groups were trained in a rectangular environment with two short white walls and two long black walls (bottom panel).

were trained on a reference memory task, with the hidden platform located consistently in one corner of the pool. When released into the pool, each rat was required to escape by finding and climbing onto the platform. Location of this platform could only be carried out by using the information provided by the rectangular shape of the arena. The corner containing the platform and the corner opposite will be referred to as the correct corners, while the remaining two corners will be referred to as incorrect. Rats were required to search in the correct corners rather than the incorrect corners. In order to ensure that the shape was the only source of information useful for finding the goal, curtains were drawn around the perimeter of the pool and the apparatus was rotated in relation to the room between trials; no cue outside the pool, therefore, had a consistent relationship with the location of the hidden platform. Additionally, the point at which the animal was released at the beginning of a trial was variable; consequently, any strategy for finding the platform based on swimming in a particular direction after release could be of little use.

Preliminary studies revealed that rats with hippocampal lesions may be particularly prone to a thigmotaxic response – swimming around the perimeter of the pool. In the experiments presented here, animals were given pre-training to forestall this strategy. Rats were initially trained to find an escape platform located in a random position in a circular pool. During this stage, the platform had a beacon attached to it. They were then trained to swim to the platform when it was consistently located in the same corner of the rectangular pool, again with the beacon attached. This beacon was not expected to overshadow learning about the shape of the environment (Pearce, Ward-Robinson, Good, Fussell, & Aydin, 2001; Hayward, McGregor, Good, & Pearce, 2003). After training in this manner, training continued with the beacon removed and the location of the hidden platform indicated only by the information provided by the shape of the environment. If the processes responsible for the use of information provided by shape take place outside the hippocampus, we might expect rats with hippocampal lesions to show comparable performance to controls on this task. On the other hand, if the hippocampus is required for orientation according to environmental shape, then rats with hippocampal lesions should show a marked impairment at correctly identifying the corner in which the platform is located.

For each trial throughout the experiment, a record was taken of the time which elapsed between the release of the rat into the pool and the rat climbing onto the platform. In addition to these latencies, the experimenter noted which corner the rat visited first on each trial – whether it was a correct or an incorrect corner. These two measures provided an assessment of rats' ability to find the platform effectively during acquisition. Because the release point of the animals varied from trial to trial during this phase, the proximity and heading direction of the platform from the release point was variable. In order to provide a measure of performance which was unaffected by this variability, test trials were given after acquisition for which no platform was present and the rat was released into the pool from its centre. During these test trials, the amount of time spent searching in each corner of the pool was recorded. If rats learn to discriminate between the corners of the rectangle, we expect that they will spend more time during this test trial searching near the correct than the incorrect corners.

Another aim of this experiment was to determine whether rats with hippocampal damage could reliably locate the platform under conditions similar to those just described when they did not need to rely on information provided by the shape of the environment. Additional groups of lesioned (the hippocampal-BW group) and control (the sham-BW group) rats were trained in a similar manner, in a rectangular arena with two short white walls and two long black (B) walls (lower panel of Figure 2). In this case, rats did not need to use any information provided by the shape of the arena in order to identify the correct corners, since they could be identified purely on the basis of the contrasting brightness of the walls. As such, if rats with hippocampal lesions are able to discriminate between correct and incorrect corners here then any deficit shown by lesioned animals trained in the white arena may be accounted for by a role for the hippocampus in processing information provided by the shape of the pool only. If, however, rats with hippocampal lesions are unable to discriminate between corners of the black and white arena, then the role of the hippocampus must extend beyond the use of information provided by shape. On the basis of previous data, rats with hippocampal lesions might be expected to choose the correct corners more often than the incorrect corners in the black and white rectangle. Morris (1982) showed that rats with hippocampal lesions were impaired at location of a hidden, but not a visible platform in an open watermaze. In this example, the visible platform provided rats with a feature which may be analogous to the feature information provided by the contrasting brightness of the walls. Similarly, then, hippocampally-lesioned rats may be able to find the platform in the black and white rectangle because the system for use of feature information is intact, but unable to locate the platform in an all-white rectangle because the neural basis for a mechanism which allows learning based on shape has been destroyed.

2. Does learning based on the rectangular shape of an environment proceed according to global or local cues?

Previous experiments have demonstrated that animals are able to orient according to information derived from the shape of environment. What is less clear is how this learning occurs. There are several ways in which animals may locate the goal, although it is worth remembering that more than one of the following strategies may be learnt simultaneously. Cheng (1986) and Gallistel (1990) have suggested that the information used by animals is a record of the shape of the *whole* environment rather than any sub-unit of it. We will refer to this type of explanation for how animals navigate with reference to the shape of the environment as the global solution, because it is the shape in its entirety which is learnt about and used to identify the location of the goal. In the rectangular watermaze, it is the rectangle which is learnt about. Another possibility, however, is that animals learn about the position of the platform in relation to some part of the shape, such as a corner. If a rat could learn to approach corners with a distinct geometric arrangement, it would be able to solve this task. To identify corners A and C (see Figure 2), for instance, the animal would need to look for a corner composed of a short wall to the left of a long wall. Doing so would disambiguate these corners from corners B and D, which are composed of a short wall to the right of a long wall. We will refer to this type of solution as the corner solution. Even more simply, corners A and C can be identified because they are situated at the left-hand ends of the two long walls; it would therefore be sufficient to learn only to swim to the left-hand ends of the long walls in order to reach these corners. We will refer to this type of solution as the individual wall solution. We have, therefore, three possible solutions for this task – the global solution, the corner solution, and the individual wall solution. Only one attempt has so far been made to discover which of these most closely resembles the learning seen in a rectangle.

Pearce, Good, Jones and McGregor (2004) trained rats to find a hidden platform located in one corner of a rectangular watermaze before placing them into a kite-shaped pool. The kite is shown in the upper panel of Figure 3. This shape is composed of a number of elements found in the rectangle. It is made up of the same two short walls and the same two long walls, but these elements are put together in a different spatial arrangement. One property which the rectangle and the kite have in common is the presence of right-angled corners. Corners A and C in the rectangle are composed of a short wall to the left of a long wall; in this way, they are geometrically similar to corner E in the kite. Likewise, corners B and D in the rectangle are similar to corner G in the kite as they are composed of a short wall to the right of a long wall. Suppose that an animal trained to search for a platform in corners A and C in the rectangle is now placed into the kite-shaped arena. The behaviour this animal would display is dependent upon the type of solution employed in the rectangle. If a global solution had been in exclusive use, the animal would not be expected to show a preference for any particular region of the kite. This is because it is the shape as a whole which is used – in a new shape, such a solution is necessarily irrelevant. More explicitly, the animal has learned where to find a platform in a rectangle but knows nothing about the new kite shape. If, however, a strategy based on some element of the arena were being used, because of the common elements between the two arenas we might expect to see some transfer of behaviour, governed by those elements. If a corner strategy were being used, for instance, the animal might be expected to approach corner E more readily than corner G because it has learned to look for the

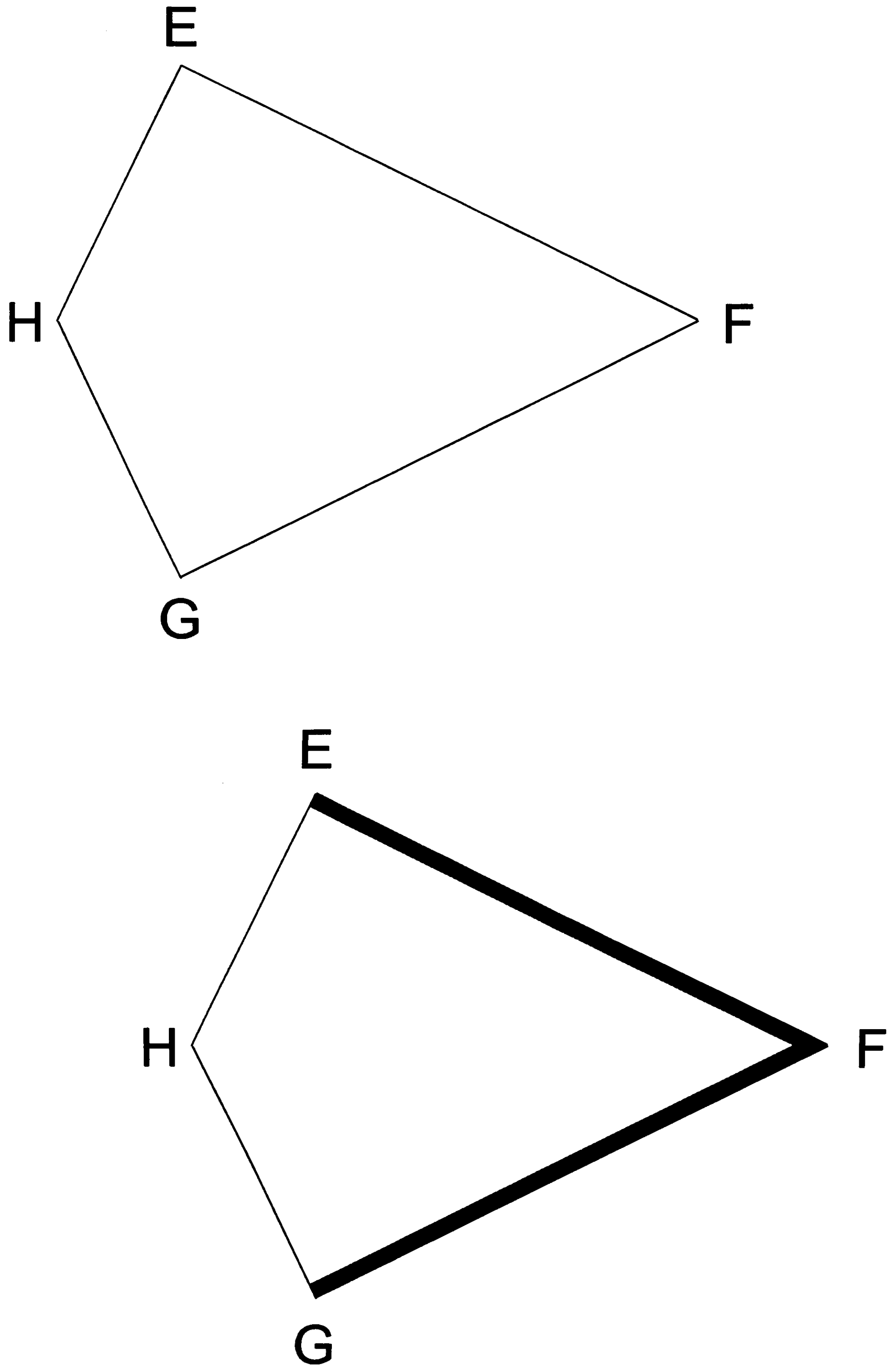

Figure 3. Schematic overhead views of the two test environments in which animals were trained during the final stage of Experiment 1. The hippocampal-W and sham-W groups were trained in a kite-shaped environment with four white walls (top panel) and the hippocampal-BW and sham-BW groups were trained in an environment of similar shape but with two short white walls and two long black walls (bottom panel).

platform in corners with a short wall to the left of a long wall. If an individual wall strategy had been in place and was based on the selection of a long wall, the animal might be expected to approach corners at the left-hand ends of the long walls; if wall EF was selected, this would lead the animal to corner E, but if wall FG was selected then the animal would go to corner F. The three possible solutions for finding the platform in one corner of the rectangle make differing predictions for how animals will behave when transferred into a kite-shaped pool.

After training rats to find a platform in one corner of a rectangular watermaze, Pearce et al. (2004) transferred those animals into the kite-shaped pool. In the kite, the platform was located in one of the two right-angled corners. For half the animals (the congruent group), the corners containing the platform in the two environments were geometrically equivalent; for the other half (the incongruent group), the two corners differed geometrically. After transfer to the kite, performance was superior for the congruent group than the incongruent group, presumably because they had learned to navigate in the rectangle by using local cues also present in the kite rather than by use of a global representation. Moreover, rats immediately showed a non-random distribution of corner entries in the kite. More frequent visits were made to the congruent right-angled corner and corner F, a pattern which is most easily explained by an individual wall strategy in the manner described above.

In Experiment 1, I assessed the use of a single wall solution in the rectangle. After training with the platform consistently located in one corner in the rectangle, animals were subsequently trained in the kite. During this second stage, the platform was located in the corner of the kite that was geometrically similar to the corner of the rectangle which contained the platform; for animals trained to find the platform in corners A and C of the rectangle, the platform was subsequently located in corner E of the kite. For animals trained to search in corners B and D in the rectangle, the platform was subsequently located in corner G of the kite. In keeping with the findings of Pearce et al., rats in the sham-W group should demonstrate a preference for searching in corner F and the correct right-angled corner at the outset of training in the kite. Training was continued for eight sessions, in order to examine whether or not this tendency persisted.

If rats in the hippocampal-W group are unable to learn to visit the correct corners in the rectangular pool, then they should show no preference for the correct over the incorrect right-angled corner when transferred into the kite. Rats trained in the black and white rectangle were transferred into a kite-shaped pool with two long black and two short white walls (lower panel of Figure 3); if these rats are able to learn to visit the correct rather than the incorrect corners in the rectangle, we might expect them to visit the correct right-angled corner more often than the incorrect right-angled corner, irrespective of whether or not they have received a hippocampal lesion.

This experiment was originally presented as part of Pearce et al. (2004), in which it was referred to as Experiment 2.

Method

Subjects. The subjects were 44 male Hooded Lister rats (*Rattus norvegicus*) supplied by Harlan (UK) Ltd. These rats were experimentally naïve, and allowed unrestricted access to food and water both before the experiment and for the duration of the experiment itself. Prior to surgery, all animals weighed between 310 and 345 g.

All were housed in pairs, in a light-proof room that was illuminated for 14.5 hr each day with its temperature maintained at 23 °C (±2 °C). The rats were tested five days a week, during the period in which the holding room was lit. At the outset of the experiment, 11 rats were assigned to each group. During the first stage of the experiment, 1 rat in the hippocampal-W group became ill and was withdrawn from the experiment.

Surgical Procedure. To produce hippocampal lesions, rats in the hippocampal-W and hippocampal-BW groups were anesthetized deeply using a mixture of isoflurane and oxygen, and placed into a stereotaxic frame (Kopf Instruments, Tujunga, CA). After reduction of the anaesthetic to a maintenance level, an incision was made along the midline of the scalp. The pericranium was retracted and the bone overlying the neocortex removed using a dental burr. Injections of neurotoxin were made using a 2-µl Hamilton syringe that was mounted on the stereotaxic frame. The plunger of the Hamilton syringe was attached to a microdrive (Model KDS 310, KD Scientific, New Hope, PA) that regulated both the rate and volume of infusion. Ibotenic acid (Biosearch Technologies, San Rafael, CA) was dissolved in phosphate-buffered saline (pH 7.4) to produce a 63-mM solution. Volumes of 0.05-0.10 µl ibotenic acid were infused at a rate of 0.03 µl/min at 28 sites (for stereotaxic co-ordinates of injection sites, see Coutureau, Galani, Gosselin, Majchrzak, & Di Scala, 1999). The Hamilton syringe was left in place for 2 min following each infusion to allow diffusion of the neurotoxin into the tissue.

Rats in the sham-W and sham-BW groups underwent a similar surgical procedure in which the skin was incised, the neocortex exposed, and the dura perforated using a standard needle, but no injection was given. The wounds of both hippocampal and sham animals were sutured following the procedure and the rats were allowed to recover from the anaesthetic in a box maintained at 30 °C. Hippocampal rats, due to the length of the procedure, were deemed likely to have suffered dehydration during surgery and were therefore given postoperative subcuticular injections of 10 ml saline and glucose solution. Because the duration of the sham surgeries was much less, rats in these groups were given no such injections. Once the rats had recovered sufficiently, they were transferred back to their home cages. A minimum of 14 days postoperative recovery were allowed before the onset of training.

Apparatus. The pool was circular, 2 m in diameter and 60 cm deep. Positioned in the centre of a room measuring 4.0 m × 3.0 m and 2.3 m high, it was mounted on a platform 0.6 m above the floor. It was filled to a depth of 29 cm with a mixture of water and 0.5 l of white opacifier E308, supplied by Roehm and Haas (UK) Ltd (Dewsbury). This mixture was changed daily and its temperature was maintained at 23 °C (±2 °C). In a white ceiling above the pool were eight 45-W spot lights, 22.5 cm in diameter, which were arranged at equal distances in a circle with its centre directly over the centre of the pool and with a diameter of 1.6 m. The spotlights were illuminated throughout the experiment. An opaque, light-blue curtain, 1.4 m high, hanging from the ceiling, was drawn completely around the pool 25 cm beyond its edge. The room was additionally illuminated by four 1.53-m strip lights, which were attached end to end in pairs on opposite walls of the room, parallel to the floor and 75 cm above the floor. There was a sliding door in the centre of one of the walls that did not support a strip light. This door provided access to an adjacent room where the experimenter would remain for the duration of each trial. A video camera with a wide-angle lens was positioned 1.75 m above the centre of the pool and 25 cm above a 30-cm diameter hole in the ceiling. The picture from the camera could be relayed to recording equipment and a PC in the adjacent room, where the pool could be observed on a TV monitor. The PC was equipped with Watermaze Software (Morris and Spooner, 1990), which could be used to analyse the movements of the rats.

The escape platform was made from clear Perspex, 10 cm in diameter, and its surface was composed of a series of concentric ridges. The platform was mounted on a column which stood on the floor of the pool so that the platform was 2.5 cm below the surface of the water. A plastic rod, 1 cm in diameter, could be screwed onto the platform 0.5 cm from its edge to form the beacon. A plastic disc 3 cm in diameter and with a thickness of 2.5 cm was attached to the top of the rod 23 cm above the surface of the water. Both the disc and the rod were coloured silver.

Four Perspex boards were used to create each rectangular pool. Two of these were 1.8 m in length and two 90 cm, all were 59 cm high and 2 mm thick. One of the longer sides of each board was attached to a bar with a square cross-section 2 cm wide, which extended beyond each end of each board by 5 cm. The boards could be suspended within the pool by resting the ends of the bars on the pool's edge. The bars attached to the longer boards overlapped with and rested on those attached to the shorter boards; therefore, whilst the top edges of the shorter boards were 33 cm above the water, the top edges of the longer boards were 35 cm above the surface. The shorter walls used to construct each rectangle were white, while the longer boards were either white or black. Two different rectangles were constructed using these boards: one was completely white, whereas the other had two short white walls, and two long black walls. The hippocampal-W and sham-W groups were trained in the white arena, while the hippocampal-BW and sham-BW groups were trained in the black and white arena. Additionally, the boards were used to construct another four-walled arena which we will refer to as the kite. This was made in a similar way to the rectangle, except that the shorter walls were now adjacent to each other, rather than opposite. Likewise, the two longer boards were now adjacent. As for the rectangular arena, all four corners of the kite made contact with the edge of the circular pool. The kite was either composed of four white walls, or two short white walls and two long black walls. As for the rectangular arena, all four corners of the kite made contact with the edge of the circular pool, with the consequence that the corners created at the points where a long and a short board met were both right-angled.

Procedure. Rats were transported to the room adjacent to the test room in groups of either five or six, in a carrying box that was placed on a shelf in the room where the experimenter remained during each trial. All rats received four sessions during pre-training. A session consisted of four trials, and in each trial a rat was required to escape from the circular pool by climbing onto the platform which had the beacon attached to it. If the rat did not find the platform within 90 s, the experimenter placed a finger directly in front of the rat's nose and guided it towards the platform (this treatment was effective with no prior training). During each trial throughout the experiment, the experimenter used a stopwatch to record the length of time between the rat being released and the rat finding the platform. Rats were allowed to remain on the platform for 15 s before their removal from the pool. After each trial, the rat was gently dried and returned to the carrying box, where it remained until the other rats had received a single trial in the pool. This cycle was repeated until all rats had received four trials. Between each of the four trials, both the platform position and the release point were changed. Both were selected at random, with the release point always somewhere on the perimeter of the pool and the rats released facing the wall.

In the rectangular arena, all sessions again consisted of four trials. Rats were released into the four-walled arena and allowed up to 90 s to locate the platform with the beacon attached to it during initial sessions. Rats failing to locate the platform were guided towards it in the manner described above. Once on the platform, rats were again left for 15 s before their removal. For all groups, the arena was rotated through 90° in a clockwise direction between each trial; for each trial in any given session, therefore, the arena was in a different orientation. Rats were released from the mid-points of the four walls, facing the wall and with the four release points selected in a random order.

Rats were trained in the rectangular arena during sessions 4-17. Rats in the hippocampal-W and sham-W groups were trained in an all-white rectangle, whereas rats in the hippocampal-BW and sham-BW groups were trained in a rectangle with two short white walls and two long black walls. For half the rats in each group, the platform was located in either corner A or corner C; for the other half, it was located in either corner B or corner D. The centre of the platform was 25 cm from the corner, along a notional line that bisected the corner. This stage of training consisted of 14 sessions, with the beacon attached for the first 4 of these. For all training trials within each of these sessions, the experimenter made a record of which corner the rat visited first upon release. A choice was considered to have been made when a rat's head entered an arc-shaped zone centred on each corner and with a radius of 40 cm; a choice, therefore, indicated that a rat had passed within 10 cm of the platform's edge. The final session of this stage consisted of three training trials of the type described above, and one test trial. This test trial was conducted with the platform removed from the pool, and all rats were allowed to swim for 60 s before they were removed from the pool. This test trial was conducted in the same rectangular arena for each rat as the previous training trials. For all test trials, watermaze software was used to track the path taken by each rat. This information was used to calculate the amount of time spent by rats in different regions of the pool. For this purpose, the pool was notionally divided into four equal quadrants, along lines which joined the mid-points of opposing walls. The percentages of time spent in the two quadrants adjacent to correct corners were combined.

The final stage of the experiment consisted of 8 sessions. During sessions 18-25, rats were trained in the kite-shaped arena. All four walls of this shape were white for the hippocampal-W and sham-W groups, while the two long walls were black for the hippocampal-BW and sham-BW groups. As in the rectangle, animals were released from the mid-points of the four walls, and the arena was rotated 90 ° between trials. For animals trained in the earlier stage with the platform in either corner A or C, the platform was now located in corner E. Rats previously trained to find the platform in corners B and D were now trained with the platform in corner G. During this stage, escape latencies and choices were scored in the same manner as during training in the rectangle. The last session consisted of three training trials and one test trial, similar to the test trial conducted at the end of the previous stage.

Results

In all statistical analyses throughout this thesis, a Type I error rate of $p < .05$ has been adopted. Unless explicitly stated, corrections are not made for multiple

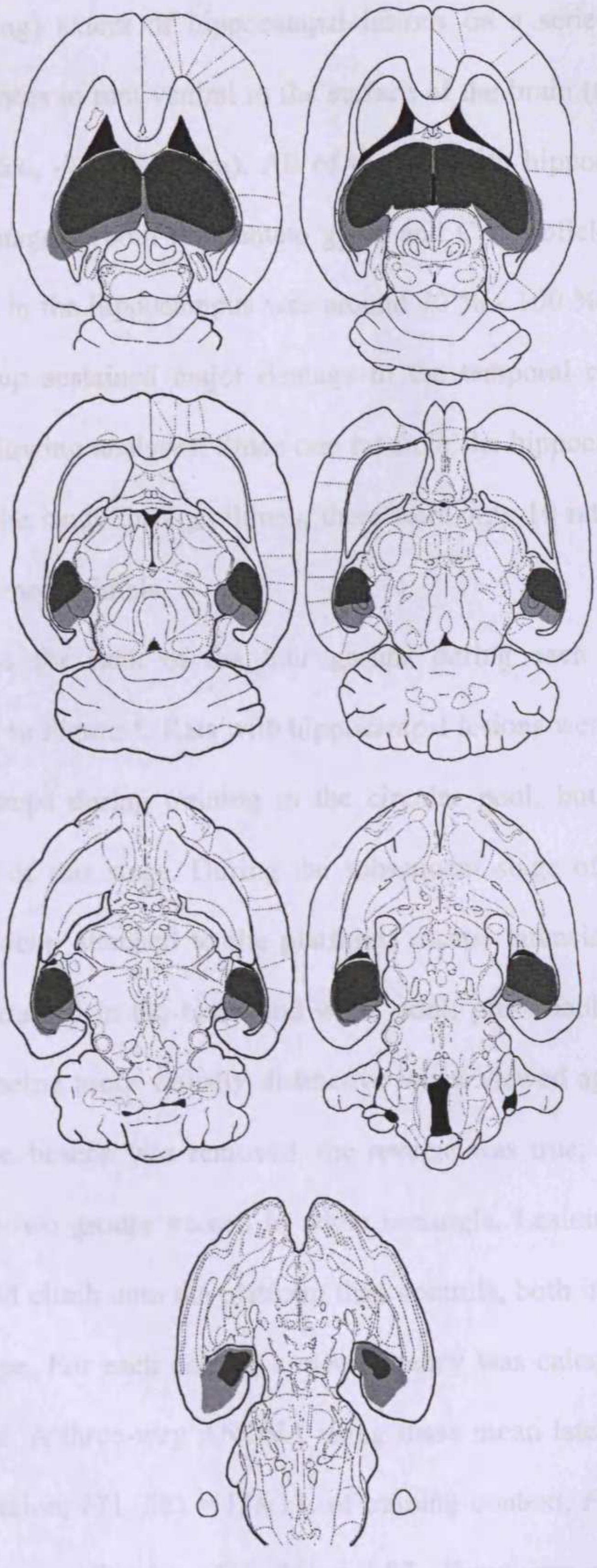

Figure 4. The maximum (light shading) and minimum (dark shading) extent of the hippocampal lesions for Experiment 1.

comparisons. Figure 4 shows reconstructions of the maximum (light shading) and minimum (dark shading) extent of hippocampal lesions on a series of horizontal sections taken at distances in mm ventral to the surface of the brain (top to bottom: -3.1, -3.6, -4.6, -5.6, -6.6, -7.6, -8.4 mm). All of the rats with hippocampal damage sustained bilateral damage to both the dentate gyrus and CA subfields at all levels. The range of cell loss in the hippocampus was around 70 % - 100 %. One rat in the hippocampal-BW group sustained major damage to the temporal cortex, and was excluded from the following analyses. Since one rat from the hippocampal-W group was withdrawn from the study through illness, there were only 10 rats in each group of hippocampally-lesioned animals.

Mean latencies for each of the four groups during each session of the experiment are shown in Figure 5. Rats with hippocampal lesions were initially much slower than other groups during training in the circular pool, but this difference narrowed by the end of this stage. During the subsequent stage of training in the rectangle with the beacon attached to the platform, escape latencies were initially longer for those rats trained in the black and white pool; presumably, this was as a result of the beacon being more visually distinctive when viewed against walls that were white. When the beacon was removed, the reverse was true; longer latencies were observed in the two groups trained in white rectangle. Lesioned animals also took longer to find and climb onto the platform than controls, both in the rectangular pool and the kite shape. For each animal, a mean latency was calculated for all the sessions in each stage. A three-way ANOVA using these mean latencies revealed a significant effect of lesion, *F*(1, 38) = 118.17; of training context, *F*(1, 38) = 35.37; but no interaction between the two, *F*(1, 38) = 1.03. There was also an effect of training stage, *F*(3, 114) = 70.52; and significant interactions with the other factors:

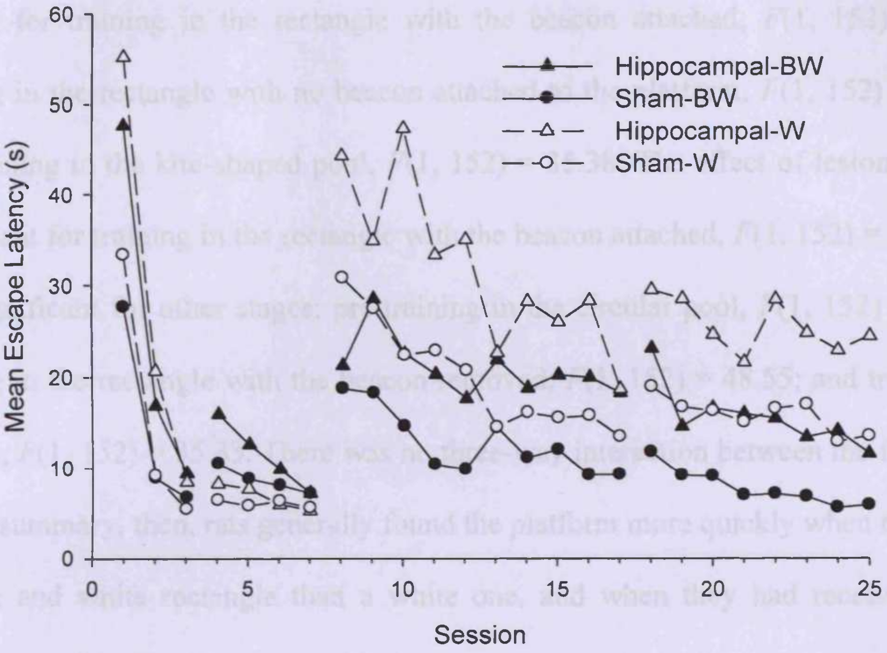

Figure 5. Mean escape latencies for the four groups of Experiment 1. Sessions 1-3 were conducted in the circular pool with the beacon attached to the platform, sessions 4-7 were conducted in the rectangular pool with the beacon attached to the platform, sessions 8-17 were in the rectangular pool with the beacon removed, and sessions 18-25 were conducted the kite-shaped pool.

Stage × Context, *F*(3, 114) = 17.48; and Stage × Lesion, *F*(3, 114) = 8.25. Simple main effects test indicated that the effect of training context was not significant for pre-training in the circular pool, *F*(1, 152) = 2.87, which occurred before the different training contexts were introduced. There was, however, a significant effect of training context for training in the rectangle with the beacon attached, *F*(1, 152) = 5.86; training in the rectangle with no beacon attached to the platform, *F*(1, 152) = 43.46; and training in the kite-shaped pool, *F*(1, 152) = 35.38. The effect of lesion was not significant for training in the rectangle with the beacon attached, *F*(1, 152) = 1.41; but was significant for other stages: pre-training in the circular pool, *F*(1, 152) = 56.13; training in the rectangle with the beacon removed, *F*(1, 152) = 48.55; and training in the kite, *F*(1, 152) = 35.33. There was no three-way interaction between the factors, *F* < 1. In summary, then, rats generally found the platform more quickly when trained in a black and white rectangle than a white one, and when they had received sham operations rather than hippocampal lesions.

Rectangular pool. We compared the performance of the groups in terms of the number of visits made to correct and incorrect corners of the pool. Figure 6 shows the percentage of trials on which the first corner visited was correct with respect to both geometry and the brightness of the walls. Because two of the four corners were both identical and equally correct for each training context, chance performance on this measure would be reflected by a score of 50 %. Within three sessions, all groups except for the hippocampal-W group were swimming directly to correct corners far more regularly than incorrect corners. The performance of the hippocampal-W group showed no improvement over the course of the trials conducted with no beacon attached to the platform. In order to assess performance at asymptote, the mean

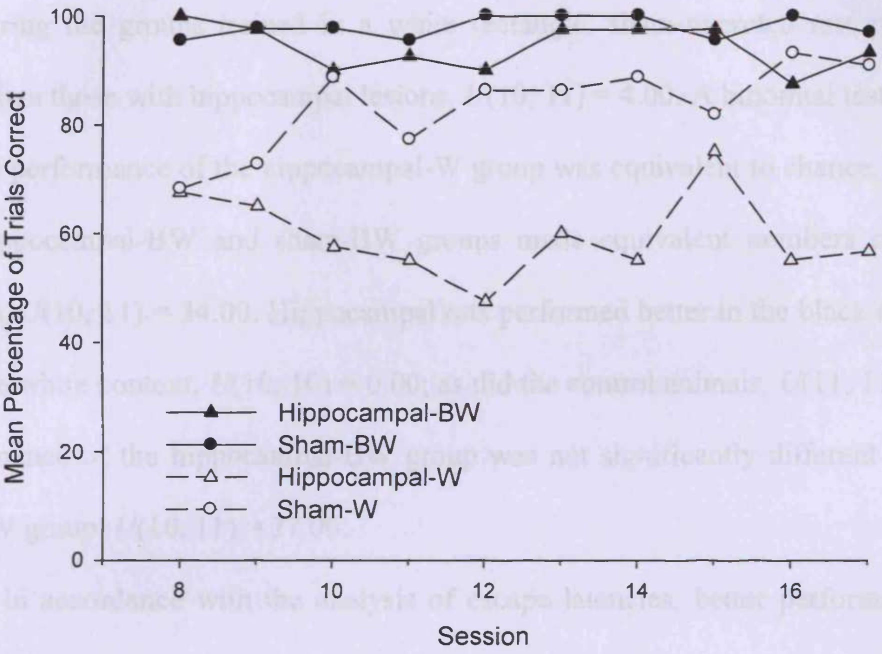

Figure 6. The mean percentage of trials on which each group entered a correct corner before an incorrect corner during each session in the rectangle in Experiment 1.

percentage of trials during the final six sessions on which each animal entered a correct corner before an incorrect corner was calculated; since these data were not continuous, non-parametric tests were used to compare groups. There was a significant overall difference between the groups, Kruskal-Wallis H(3, 42) = 29.45. Comparing the groups trained in a white rectangle, sham-operated rats performed better than those with hippocampal lesions, $U(10, 11) = 4.00$. A binomial test revealed that the performance of the hippocampal-W group was equivalent to chance, $p = 0.18$. The hippocampal-BW and sham-BW groups made equivalent numbers of correct choices, $U(10, 11) = 34.00$. Hippocampal rats performed better in the black and white than the white context, $U(10, 10) = 0.00$; as did the control animals, $U(11, 11) = 9.50$. Performance of the hippocampal-BW group was not significantly different from the sham-W group, $U(10, 11) = 27.00$.

In accordance with the analysis of escape latencies, better performance was observed for groups trained in the black and white than white rectangle for both lesioned and control animals. One difference between the two analyses, however, is the comparison of the hippocampal-BW and sham-BW groups. The lesioned rats were slower to find the platform than the controls, but both groups made initial entries to correct corners on an equivalent number of trials. One explanation for this discrepancy could be some general impairment of swim velocity in the hippocampal-BW group. Another possibility is that the lack of a difference between corner entry performances reflects an insensitivity of the test. This possibility is made more credible by the results of the probe trial carried out during Session 17. The hippocampal-BW group spent 68.04 % of the trial in the correct pair of quadrants, while for the sham-BW group this figure is 72.28 %. In the white arena, lesioned animals spend 54.49 % of the trial in the correct pair of quadrants, whereas controls spent 64.93 % of the trial in correct quadrants. As such, lesioned animals performed more poorly than controls in both arenas. A two-way ANOVA of the mean percentages of time spent in the correct pair of quadrants reveals an effect of training context, $F(1, 38) = 12.16$; of lesion, $F(1, 38) = 6.00$; but no interaction between these factors, $F(1, 38) = 1.07$. The lack of interaction suggests that the impairment resulting from hippocampal lesions was equally large in both the white and the black and white rectangles.

Despite showing a deficit in comparison to the sham-BW group, the impairment observed in the hippocampal-BW group was not absolute. A binomial test showed that lesioned rats were able to visit the correct corners far more frequently than the incorrect corners, $p = 0.02$; and a one-sample t-test demonstrated that they spent more time searching in the correct two quadrants combined during the test trial than would be expected by chance, $t(9) = 5.79$. These results indicate that, in the black and white arena, lesioned rats were not unable to learn about the position of the platform in relation to the walls of the arena *per se*; they were simply not as good as the control animals at this task. In the case of the sham-BW group, we would expect them to visit the correct more than the incorrect corners by virtue of both its geometry and the information provided by the brightness of the walls. For the hippocampal group, there are two possible explanations for their tendency to visit the correct corners more often than the incorrect corners. The first is that these animals were able to use information provided by the shape of the arena; given other results, including those from the hippocampal-W group here, this does not seem likely. The alternative is that they were able to identify the correct corners only on the basis of the information provided by the brightness of the walls, and were unable to use the information provided by the rectangular shape of the arena. While rats in the hippocampal-BW group may have been able to learn about the position of the platform in this way, they were still impaired in relation to the sham-BW group, possibly as a result of the lesioned animals being able to use less of the available information than the controls. According to this explanation, results from groups trained in a white-walled arena can be accounted for easily; if the hippocampus is necessary for learning based on information provided by shape, then rats with hippocampal lesions will necessarily be impaired on a task which can be solved exclusively by the use of such information.

In both contexts, then, control animals outperformed lesioned rats. This, as we have suggested, may have been due to the presence of geometric information, which could be used only by controls. An additional possibility, however, is that hippocampal lesions resulted in some general impairment which applied to both tasks. If this were true, we would not need to propose any role for the hippocampus that is specific to information provided by the shape of the environment. In opposition to this possibility, McGregor, Hayward, Pearce and Good (2004) have conducted a reference memory task in which lesioned and control animals were trained in a rectangle with feature information available, before being tested in a square arena. The square preserved the feature information present in the rectangle, but gave no geometric clues to the location of the platform. During training in the rectangle, lesioned animals were inferior to controls. In the test phase, however, performance of the two groups was identical. This suggests that lesions of the hippocampus did not disrupt performance on a task which was solvable only by feature information, but did result in a deficit when geometric cues were additionally available. This dissociation between geometric and feature information is consistent with the idea that the hippocampal-BW group of Experiment 1 performed more poorly than the sham-BW group not because they were generally impaired but because they were able to use only one of the two types of information present.

Kite-shaped pool. During training in the kite-shaped pool, the groups differed greatly in the distribution of their corner entries. The sham-BW group (Figure 7) rapidly learned to go to the correct right-angled corner, while none of the other groups did. Both the sham-W (Figure 8) and the hippocampal-BW (Figure 9) groups made persistent errors to corner F throughout training, visiting this corner as often as the correct right-angled corner (see Figure 3). The hippocampal-W group (Figure 10) visited corners E, F, and G with roughly equal frequency. None of the groups made any substantial amount of choices to the obtuse angled corner, H.

Considering the mean number of entries made to each corner during the last six non-test sessions (i.e. sessions 19-24), the sham-BW group displayed a distribution of choices that was different to that which would be expected by chance, Friedman $\chi^2(3, 11) = 30.45$. The number of choices made to the incorrect right-angled corner was less than the number made to the correct right-angled corner, Wilcoxon $T(11) = 0$, or to corner F, $T(10) = 0$. The number of entries to the corner H was also less than the number made to either the correct corner or corner F, Ts(11) =0. The number made to corner H and the incorrect right-angled corner was equivalent, with nine rats choosing the incorrect right-angled corner and corner H with equal frequency. Overall, however, the entries were dominated by those made to either the correct right-angled corner or the apex. These corners were visited with equal frequency on the first session in the kite, but during the subsequent six sessions animals developed a significant tendency to visit the correct corner more often than the apex, $T(11) = 1.50$.

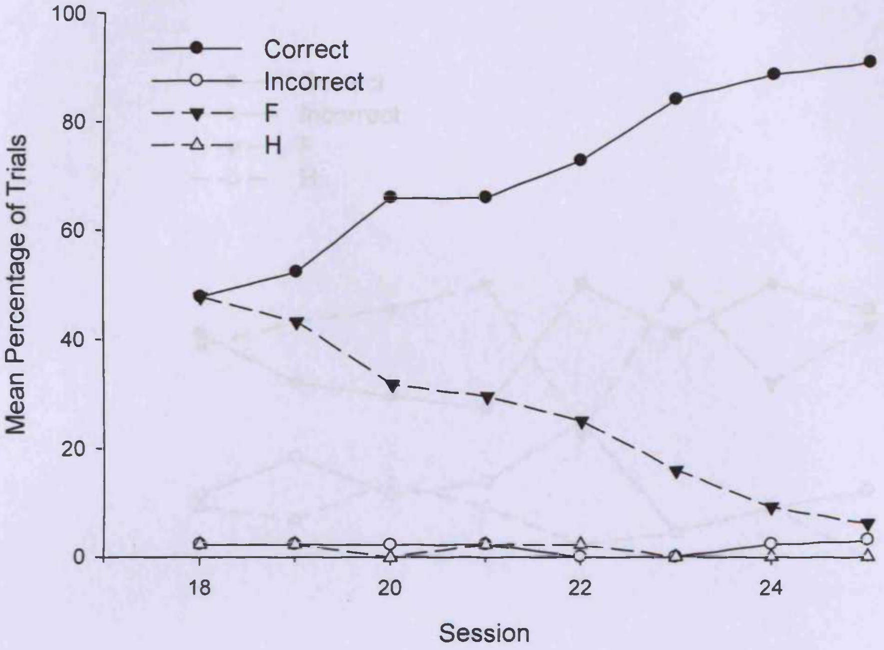

Figure 7. The distribution of choices for rats in the Sham-BW group of Experiment 1 during sessions in the kite. Correct = the right-angled corner containing the platform; Incorrect = the right-angled corner not containing the platform; F = corner F; H = corner H (see Figure 3).

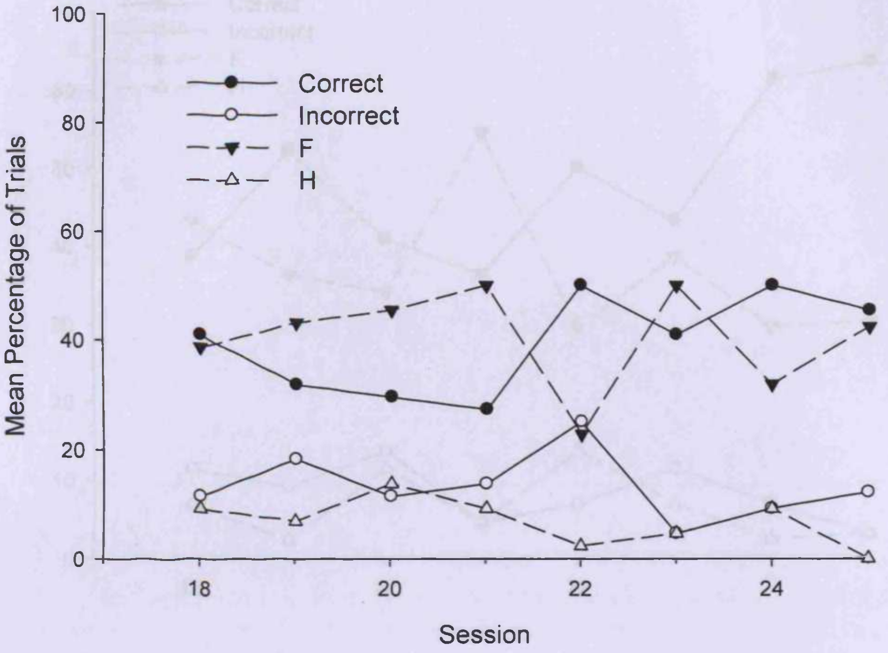

Figure 8. The distribution of choices for rats in the Sham-W group of Experiment 1 during sessions in the kite. Correct = the right-angled corner containing the platform; Incorrect = the right-angled corner not containing the platform; F = corner F; H = corner H (see Figure 3).

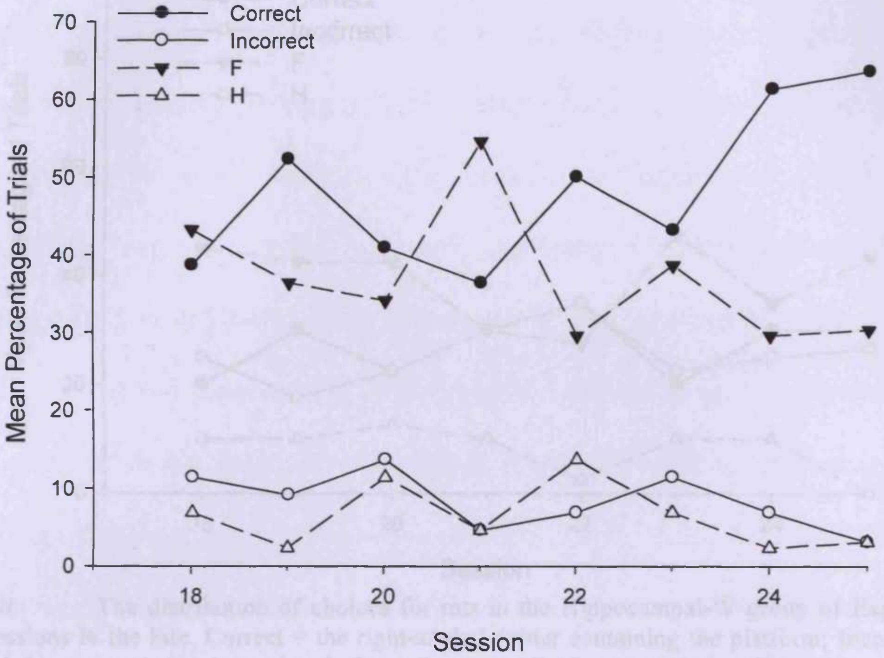

Figure 9. The distribution of choices for rats in the Hippocampal-BW group of Experiment 1 during sessions in the kite. Correct = the right-angled corner containing the platform; Incorrect = the right-angled corner not containing the platform; F = corner F; H = corner H (see Figure 3).

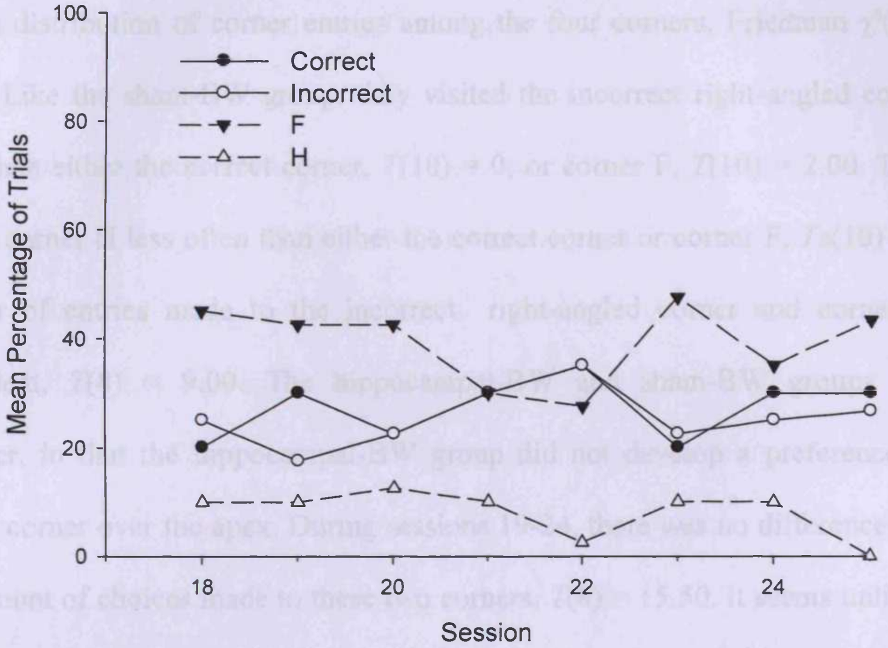

Figure 10. The distribution of choices for rats in the Hippocampal-W group of Experiment 1 during sessions in the kite. Correct = the right-angled corner containing the platform; Incorrect = the right-angled corner not containing the platform; F = corner F; H = corner H (see Figure 3).

A quick glance at the distribution of choices for the hippocampal-BW group reveals a tendency for these rats to visit the correct right-angled corner and the acute angled corner F more frequently than the remaining two corners. Indeed, this group had an uneven distribution of corner entries among the four corners, Friedman $\chi^2(3, 10) = 23.14$. Like the sham-BW group, they visited the incorrect right-angled corner less often than either the correct corner, *T*(10) = 0; or corner F, *T*(10) = 2.00. They also visited corner H less often than either the correct corner or corner F, *T*s(10) = 0. The number of entries made to the incorrect right-angled corner and corner H was equivalent, *T*(8) = 9.00. The hippocampal-BW and sham-BW groups differed, however, in that the hippocampal-BW group did not develop a preference for the correct corner over the apex. During sessions 19-24, there was no difference between the amount of choices made to these two corners, *T*(8) = 15.50. It seems unlikely that these rats would be unable to tell these two corners apart, since they differ in both the angle between the walls and the brightness of the walls - the correct corner is composed of one white and one black wall intersecting at an angle of 90 °, whereas the apex is an acute angle composed of two black walls. One common feature of the two corners, however, is that they are both located at the left-hand end of a long wall. In the case of corner E, it is at the left-hand end of side EF; in the case of corner F, it is at the left-hand end of side FG. If location of the platform in the rectangle were carried out by searching at the left-hand ends of the long walls, transfer of this behaviour to the kite-shaped arena would necessarily lead to equally frequent visits to corners E and F. This transfer of behaviour provides a possible explanation for the equal number of entries by the sham-BW group to corners E and F on the first session in the kite. Importantly, though, the sham-BW group subsequently learned to visit corner E much more often than corner F; a result which suggests that they were able to develop some new strategy for locating the platform, one which was more appropriate for locating the platform in the kite and did not result in frequent errors. The fact that the hippocampal-BW group continued to visit corner F as often as corner E suggests either that they were unable to acquire this new strategy, or that they were simply more rigidly persevering with the old one. Our results cannot differentiate between these two possibilities, and we are unable to reject either. As previously noted, however, it seems unlikely that these rats could not differentiate between corners E and F. It seems more credible, therefore, that the hippocampal-BW group experienced greater difficulty than the sham-BW group in changing their strategy from one that was effective in the rectangular arena to one that is more appropriate for the kite.

This difficulty in shifting strategy was also evident in the sham-W group. First choices in each trial for this group were unevenly distributed between the four corners of the kite, Friedman $\chi^2(3, 11) = 26.06$. The number of choices made to corner H was less than the number made to either the correct right-angled corner or corner F, *T*s(11) = 0. The number of initial entries to the incorrect right-angled corner was also less than the number made to either the correct right-angled corner, *T*(11) = 1.50; or corner F, *T*(11) = 0. The number made to the incorrect right-angled corner and corner H was equivalent, *T*(10) = 9.50. The correct right-angled corner and corner F were visited on an equivalent number of trials, *T*(11) = 27.50. This failure of the sham-W group to go to the correct right-angled corner more often than corner F can be explained by similar arguments to those proposed for the hippocampal-BW group. One way in which the two corners are similar is that each one is situated at the left-hand end of a long wall. If navigation in the rectangle were conducted by searching at the left-hand ends of the long walls, transfer of this behaviour to the kite-shaped arena would result in an equal number of choices to corner F as to the correct right-angled corner. As noted for the hippocampal-BW group, the persistence of these errors in the kite suggests that a newer, more appropriate strategy was not adopted. Once again, we are unable to say on the basis of these results if this was because the animals cannot tell the correct right-angled corner and corner F apart, or if they simply failed to change their behaviour to use a strategy of which they should be capable. A final possibility is that rats had an unconditioned preference for corner F. This, coupled with accurate discrimination of the correct right-angled corner from others, could produce the distribution of corner choices seen in the sham-W group, the hippocampal-BW group, and the first session following transfer for the sham-BW group. The subsequent good performance of the sham-BW group may be due to the diminishing of this unconditioned preference.

The hippocampal-W group also distributed their choices between the four corners in a manner unlike that which we might expect by chance, Friedman $\chi^2(3, 10) = 18.70$. This group made the highest number of initial entries to corner F. The number made here was higher than for the correct right-angled corner, $T(9) = 3.00$; the incorrect right-angled corner, $T(10) = 3.00$; and corner H, $T(10) = 0$. The number of entries to corner H was less than that for each of the correct right-angled corner, $T(10) = 1.50$; and the incorrect right-angled corner, $T(10) = 5.50$. The proportion of trials on which the animal initially visited each of the right-angled corners was equivalent, $T(10) = 20.00$. Since this group were severely impaired in the rectangular arena when compared to the other groups, it is perhaps not surprising that they showed no preference for the correct over the incorrect right-angled corner. What is more surprising, however, is that they visited the acute angle F more often than any other corner. The reason for this is unclear, though it is possible that they may have a natural tendency to head towards this corner when they are lost. An affinity to head towards an enclosed space in times of stress may mean that this group, lacking a reliable strategy for locating the platform, were more attracted to the narrow area at the corner F than any other region. Such explanations, however, are speculative, and cannot be confirmed by present data. What is clear is that not only did the hippocampal-W group make a high number of errors, but that these errors were not confined to corner F; it is unlikely, therefore, that they were as a result of similar tactics to the errors observed in the hippocampal-BW and sham-W groups. It is worth noting at this stage that rats in the hippocampal-W group may have performed poorly in the kite not solely because they had learned little about the location of the platform in the rectangle, but also because the hippocampus may have some role in the transfer of behaviour from one shape to another. Tommasi and Save (2005) trained rats to locate a hidden goal in the centre of a square arena, before testing animals in novel environments. While controls frequently searched in the centres of the new arenas, rats with hippocampal lesions did so less often. Despite this, they were not impaired at locating the goal in the original square arena. When transferred, then, they did not adapt to the new environments in the same way and to the same degree as controls. If a similar principle applied in the current experiment, we might not expect rats in the hippocampal-W group to show close transfer of behaviour from the rectangle to the kite-shaped arena; for this reason, the results of principle interest in this group are those obtained in the rectangular environment.

During sessions 19-24, there was an overall difference between the number of choices made to the correct corner by the four groups, Kruskal-Wallis H(3, 42) = 28.09. The sham-BW group made more frequent correct entries than the hippocampal-BW group, *U*(10, 11) = 9.00. There was also a poorer performance by the hippocampal-W group than the sham-W group, $U(10, 11) = 21.50$. Those trained in the black and white arena made more correct choices than those trained in a white arena, both for the lesioned animals, $U(10, 10) = 7.50$; and for the shams, $U(11, 11) = 4.50$. This is consistent with the results of the probe trial carried out during the final session. In the case of a probe trial carried out in the kite, there is only one correct quadrant. The amount of time during this trial that was spent in the correct quadrant, as a percentage of the amount of time spent in the correct and incorrect quadrants combined, was: for the hippocampal-BW group, 71.12 %; for the sham-BW group, 80.87 %; for the hippocampal-W group, 52.39 %; and for the sham-W group, 64.67 %. A two-way ANOVA revealed an effect of training context, $F(1, 38) = 25.19$; of lesion, $F(1, 38) = 8.78$; but no interaction between these factors, $F < 1$. The effect of the lesions is therefore equally large for both the white and the black and white training contexts.

In summary, the results from the sham-W group demonstrate that learning based on information provided by the shape of the rectangular arena influenced subsequent behaviour in the kite; this finding suggests that orientation in the initial environment was not dependent upon a global representation. This finding is consistent with those reported by Pearce et al, who demonstrated a similar transfer of learning from a rectangular to a kite-shaped pool. The results from the groups of lesioned animals show that, while the hippocampus was necessary for the use of the information provided by the shape of the environment, it was not critical for the use of feature information provided by the brightness of the walls of the arena. Rats in the hippocampal-BW group learned to swim to a particular corner of the rectangle on the basis of the brightness of the walls, indicating that this ability is not dependent upon the hippocampus. Rather, the hippocampus is required for orientation based on information provided by the shape of the rectangular arena. Since the sham-W group did not orient according to a global representation in the rectangle, the deficit shown by the hippocampal-W group strongly suggests a role for the hippocampus in navigation based on local cues provided by shape. This finding is in direct conflict with the idea that the hippocampus is critical for navigation because it is the neural basis of a global representation.

EXPERIMENT 2

In Experiment 1, the hippocampal-W and sham-W groups failed to demonstrate reliably that they could learn to visit the correct corner during the final stage of training in the kite-shaped arena. In the case of the sham-W group, persistent errors were made to corner F (see Figure 3), the acute-angled corner; the hippocampal-W group visited corners E, F and G equally often. As noted earlier, there are two possible explanations for this failure. The first is that these rats were unable to discriminate between these corners, and so could not learn to regularly visit one more than another. The second possibility is that they did not have difficulty discriminating between the corners *per se*, but that the previous training stage in the rectangular pool exerted some influence over subsequent behaviour that led to these errors. In order to better understand the results from Experiment 1, we must try to differentiate between these accounts. In Experiment 2, therefore, a group of lesioned animals (the hippocampal-90 group) and a group of control animals (the sham-90 group) were trained to locate a platform hidden in one of the right-angled (90) corners of the white kite, with no prior training in the rectangular pool. If these animals make errors akin to those made by the hippocampal-W and sham-W groups of Experiment 1 during the kite stage of that experiment, then an explanation for those errors which is based upon the influence of previous training in the rectangle can be ruled out. As such, frequent errors in the current experiment may suggest that the animals are simply unable to learn to visit the correct corner in the kite-shaped arena. Such a finding would contradict the findings of Pearce et al. (2004), in which rats were successfully trained to visit the correct corner in a kite-shaped pool.

If animals are not able to learn to visit the correct corner in the kite, one possible interpretation of the results could be that the shape of the pool is not sufficiently distinctive to provide information allowing areas to be differentiated. To examine this possibility, additional groups of lesioned (the hippocampal-F group) and control (the sham-F group) animals were trained to find a hidden platform located in corner F. Good performance by these groups would demonstrate that corner F is not indiscriminable from the other corners, and that the shape of the arena is distinctive enough to allow learning on that basis. Any failure by the hippocampal-90 and sham-90 groups to visit the correct corner reliably could not, therefore, be explained in such a way.

Another purpose of the current experiment was to extend the generality of the transfer effect found in Experiment 1. In that experiment, animals were trained to find the platform in a rectangle, before being trained in a kite-shaped pool. Behaviour in the kite suggested that prior experience gained in the rectangle was influential after transfer; in the current experiment, the animals were trained from the outset in the kite. After this training, they were tested in a rectangular arena. If a transfer effect occurs, the distribution of choices between the corners of the rectangle will be influenced by prior experience. Those animals trained to search for the platform in corner F will not be tested in the rectangle, since corner F is equally similar to each corner of the rectangle. For animals trained to find the platform in right-angled corners in the kite, however, more choices may occur at those corners in the rectangle which are similar to the correct corner in the kite. An animal trained to search in corner E in the kite, for instance, may show a preference for corners A and C in the rectangle, since these corners are similar to corner E geometrically.

Method

Subjects and apparatus. The subjects were 44 male Hooded Lister rats, housed in the same manner as those in Experiment 1. Twelve rats were assigned to each of the hippocampal-90 and hippocampal-F groups, all of which were given lesions of the hippocampus according to the same method as for Experiment 1. Ten rats were assigned to each of the sham-90 and sham-F groups, all of which were given control operations of the type previously described.

The apparatus was the same as in previous Experiment 1, with white boards used to create a kite in the principal stage of the experiment and a rectangle in final test sessions, as described below.

Procedure. Rats were transported to the room adjacent to the test room in groups of either five or six. All rats received five sessions of pre-training in the circular pool, in the manner previously described. In the experiment proper, all sessions again consisted of four trials. Rats were released into the kite-shaped arena and allowed up to 90 s to locate the platform with the beacon attached to it during sessions 6-9 only. The platform was consistently located 25 cm from the relevant corner, along the notional bisector of that corner. For the hippocampal-F and sham-F groups, the platform was located in corner F. For the hippocampal-90 and sham-90 groups, the platform was located at either corner E or corner G. For all groups, the kite was rotated through 90 ° in a clockwise direction between each trial; rats were released from the mid-point of each wall once during each session. Rats then received twelve sessions in the kite with no beacon attached to the platform. Apart from the absence of the stick, the protocol for these sessions was identical to that used for the first four sessions of training in the kite. The last of these sessions, session 21, involved three training trials in the kite and a test trial in a rectangular pool; rats were released from the centre of the rectangle and allowed to search the arena freely for 60 s.

For sessions 22 and 23, the hippocampal-90 and sham-90 groups were given four training trials per session in the rectangular pool. In this case, the platform was located 25 cm from a corner which had the same geometric properties as the correct corner in the kite; for rats trained with the platform in corner E of the kite, the platform was located in corner A of the rectangle, and rats trained with the platform at G in the kite were subsequently trained with the platform at B in the rectangle.

Procedural details that have been omitted, including scoring of choice data, were the same as for Experiment 1.

Results

Figure 11 shows reconstructions of the maximum (light shading) and minimum (dark shading) extent of the hippocampal lesions on a series of horizontal sections taken at distances in mm ventral to the surface of the brain (top to bottom: -3.1, -3.6, -4.6, -5.6, -6.6, -7.6, -8.4 mm). Three rats with hippocampal lesions had cell loss of below 50 % in the hippocampus, and were excluded from the study. The remaining rats sustained hippocampal cell loss of around 75 % - 100 %; after selection, there were 11 rats in the hippocampal-90 group, and 10 rats in the hippocampal-F group. All rats sustained some cell loss in the subiculum, most evident in ventral areas.

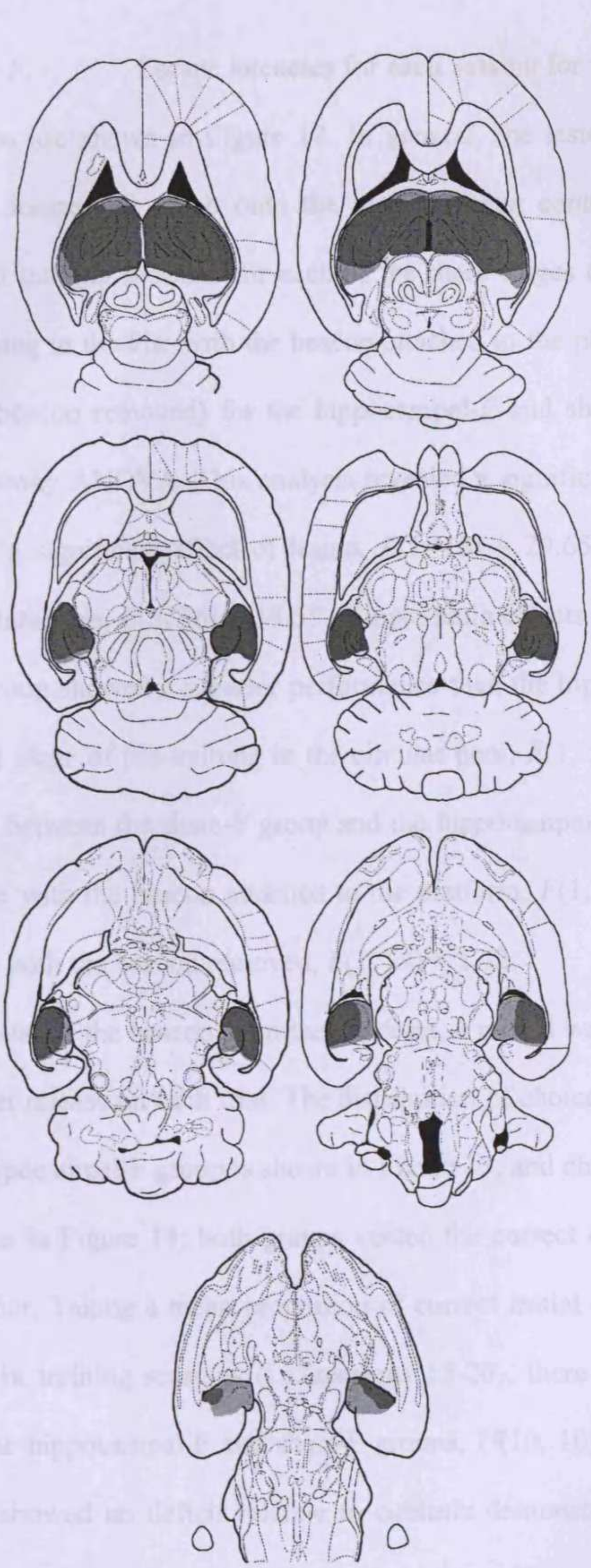

Figure 11. The maximum (light shading) and minimum (dark shading) extent of the hippocampal lesions for Experiment 2.

Training to corner F. Escape latencies for each session for the hippocampal-F and sham-F groups are shown in Figure 12. In general, the lesioned animals took slightly longer to locate and climb onto the platform than controls. Mean escape latencies across all training sessions for each of the three stages (pre-training in the circular pool, training in the kite with the beacon attached to the platform, training in the kite with the beacon removed) for the hippocampal-F and sham-F groups were entered into a two-way ANOVA. This analysis revealed a significant effect of stage, $F(2, 36) = 75.80$; a significant effect of lesion, $F(1, 18) = 29.65$; and a significant Stage × Lesion interaction, $F(2, 36) = 14.55$. Simple main effects tests demonstrated that the sham-F group showed a superior performance than the hippocampal-F group only for the initial stage of pre-training in the circular pool, $F(1, 54) = 57.72$. There was no difference between the sham-F group and the hippocampal-F group either for training in the kite with the beacon attached to the platform, $F(1, 54) = 1.43$; or for training in the kite with the beacon removed, $F(1, 54) = 1.42$.

After removal of the beacon from the platform, a record was taken of the first corner entered after release on each trial. The distribution of choices between the four corners for the hippocampal-F group is shown in Figure 13, and choices for the sham-F group are shown in Figure 14; both groups visited the correct corner, F, far more often than any other. Taking a mean proportion of correct initial entries for each rat during the final six training sessions (i.e. sessions 15-20), there was no difference between rats in the hippocampal-F and sham-F groups, $U(10, 10) = 30.00$. That the lesioned animals showed no deficit relative to controls demonstrates that rats with lesions of the hippocampus were able to navigate in this white walled arena with no impairment, at least under these conditions. Rats in both groups were able to correctly identify corner F, although it is less clear how they did this. One explanation is that

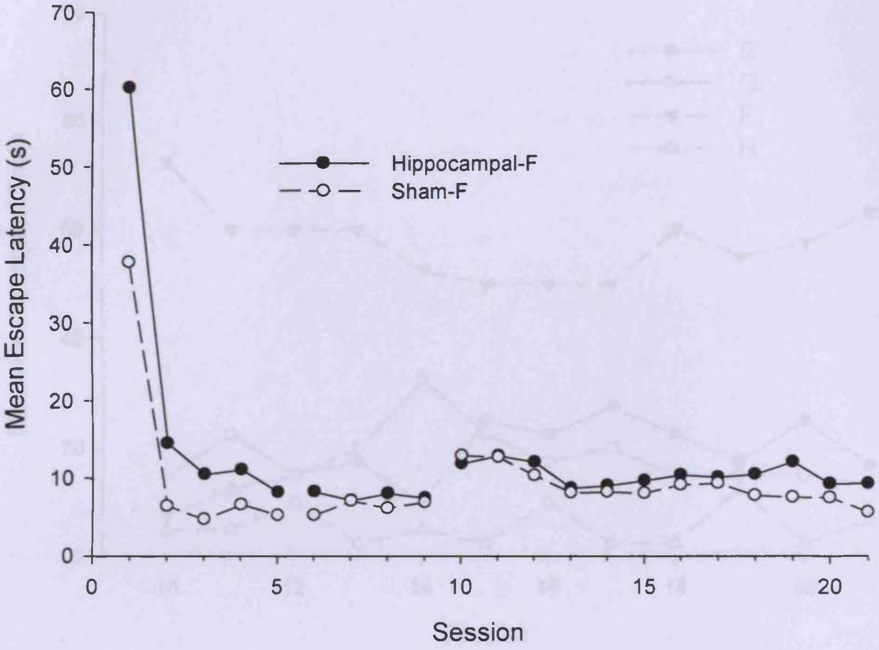

Figure 12. Mean escape latencies for the hippocampal-F and sham-F groups of Experiment 2. Sessions 1-5 were conducted in the circular pool with the beacon attached to the platform, sessions 6-9 were conducted in the kite-shaped pool with the beacon attached to the platform, and sessions 10-21 were conducted the kite-shaped pool with the beacon removed.

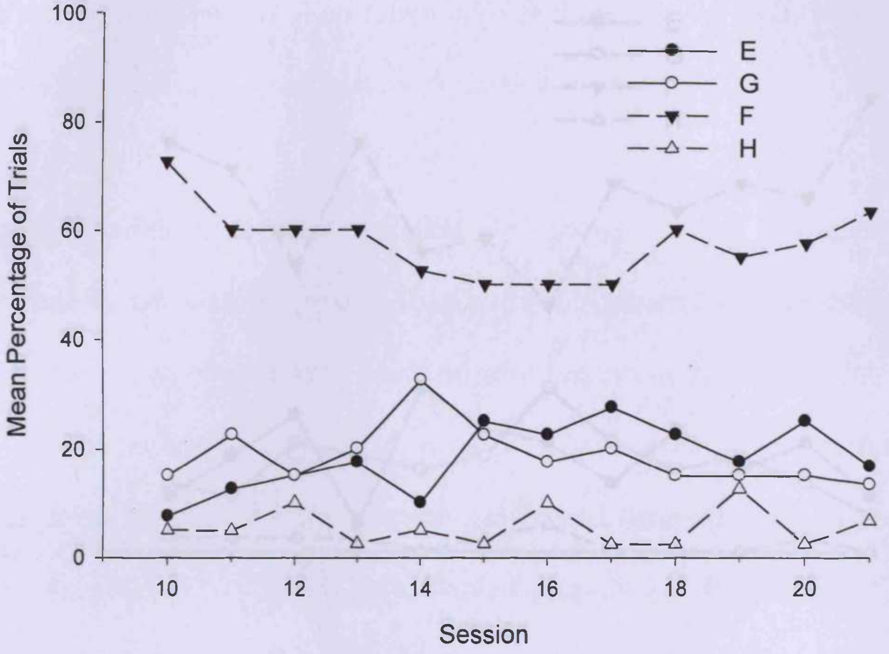

Figure 13. The mean percentage of trials on which the hippocampal-F group of Experiment 2 visited each of corners E, F, G, and H during training (see Figure 3).

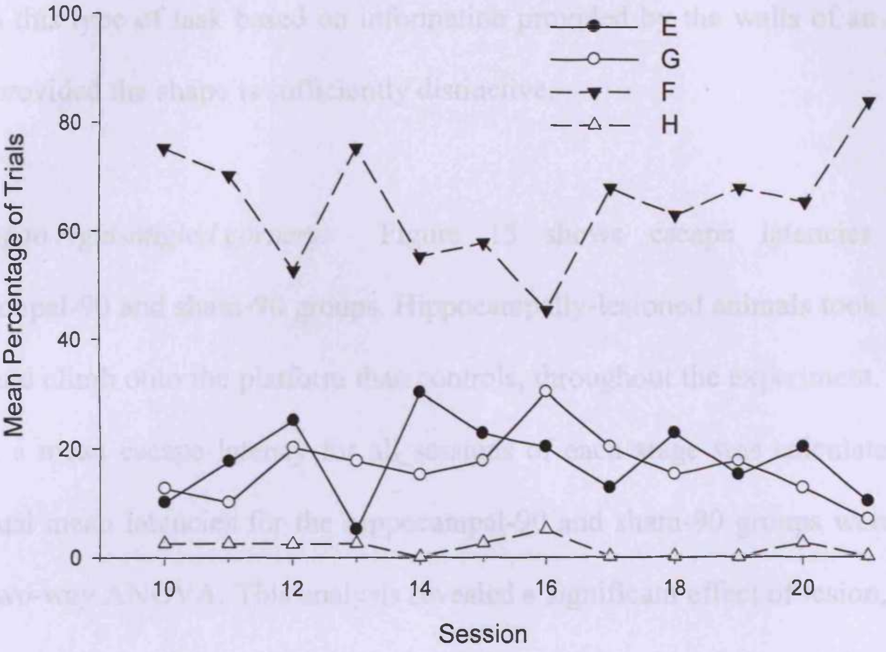

Figure 14. The mean percentage of trials on which the sham-F group of Experiment 2 visited each of corners E, F, G, and H during training (see Figure 3).

rats were able to discriminate between the angles of the different corners, since corner F was the only corner at which the angle subtended by the walls was acute. Another possibility is that rats identified corner F because it was the only corner composed of two long walls. In either case, it is clear that rats with hipppocampal lesions are able to learn this type of task based on information provided by the walls of an all-white arena, provided the shape is sufficiently distinctive.

Training to right-angled corners. Figure 15 shows escape latencies for the hippocampal-90 and sham-90 groups. Hippocampally-lesioned animals took longer to locate and climb onto the platform than controls, throughout the experiment. For each animal, a mean escape latency for all sessions of each stage was calculated. These individual mean latencies for the hippocampal-90 and sham-90 groups were entered into a two-way ANOVA. This analysis revealed a significant effect of lesion, $F(1, 19) = 33.04$; an effect of stage, $F(3, 57) = 41.86$; but no interaction between the two, $F(3, 57) = 1.90$. The distribution of choices between the four corners of the arena during the training stage in the kite is shown for the hippocampal-90 group in Figure 16, and for the sham-90 group in Figure 17. Generally speaking, by the end of training more visits were made by the sham-90 group to the correct right-angled corner than any other, whereas the hippocampal-90 group continued to make visits to the incorrect right-angled corner, and the acute angle F. The sham-90 group distributed their initial corner entries during the final six session in the kite unevenly, Friedman $\chi^2(3, 10) = 20.41$. More choices were made to the correct corner than each of the incorrect right-angled corner, $T(10) = 4.00$; corner F, $T(9) = 0$; and corner H, $T(10) = 0$. They also made fewer entries to corner H than corner F, $T(9) = 0$; and the incorrect right-angled corner, $T(9) = 1.00$. The number of choices made to the incorrect right-angled

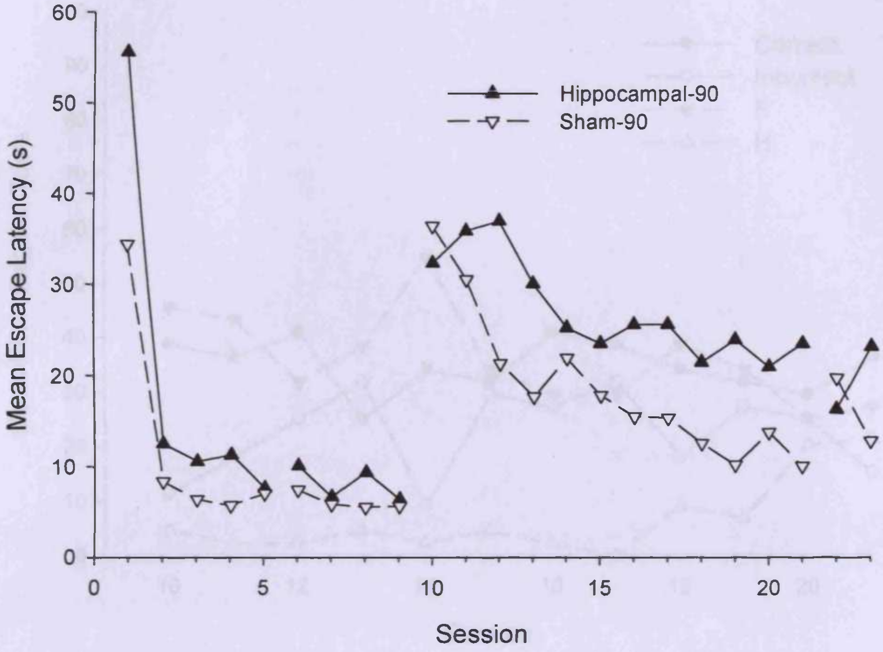

Figure 15. Mean escape latencies for the hippocampal-90 and sham-90 groups of Experiment 2. Sessions 1-5 were conducted in the circular pool with the beacon attached to the platform, sessions 6-9 were conducted in the kite-shaped pool with the beacon attached, sessions 10-21 were conducted the kite-shaped pool with the beacon removed, and sessions 22 and 23 were conducted in the rectangular pool.

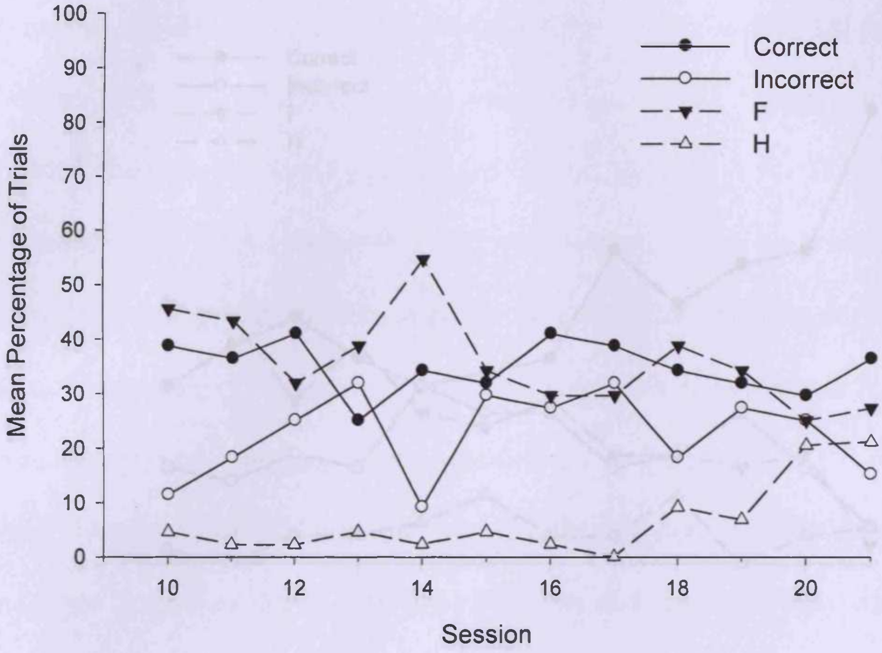

Figure 16. The distribution of choices for rats in the hippocampal-90 group of Experiment 2 during training sessions in the kite-shaped pool.

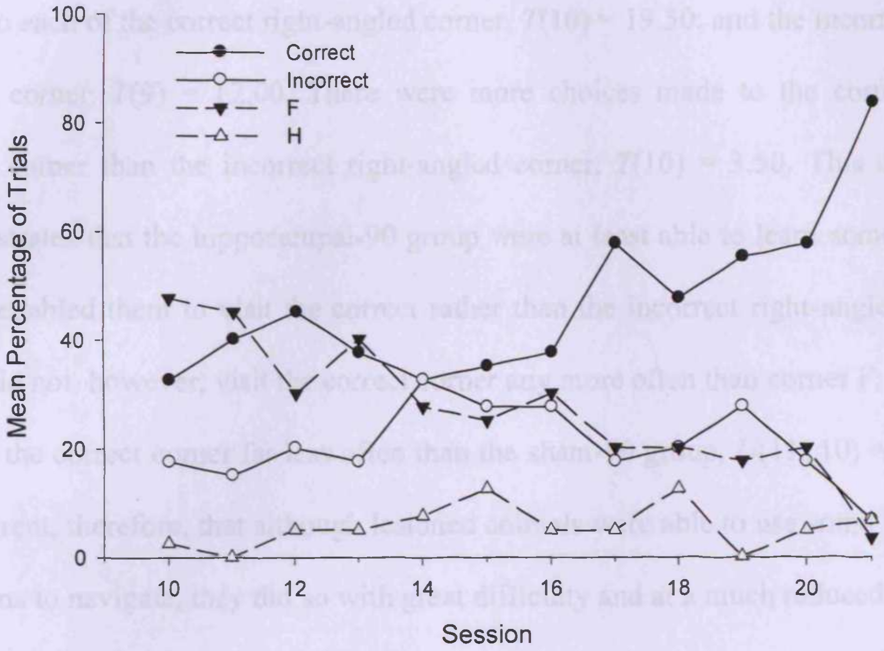

Figure 17. The distribution of choices for rats in the sham-90 group of Experiment 2 during training sessions in the kite-shaped pool.

corner and corner F was equivalent, *T*(9) = 21.50. The hippocampal-90 group also had a non-random distribution of choices among the four corners, Friedman $\chi^2(3, 11)$ = 23.86. Fewer choices were made to corner H than each of the other corners, *T*s(11) = 0. The number of entries made to the acute angle F was equivalent to the number made to each of the correct right-angled corner, *T*(10) = 19.50; and the incorrect right-angled corner, *T*(9) = 12.00. There were more choices made to the correct right-angled corner than the incorrect right-angled corner, *T*(10) = 3.50. This difference demonstrates that the hippocampal-90 group were at least able to learn some strategy which enabled them to visit the correct rather than the incorrect right-angled corner. They did not, however, visit the correct corner any more often than corner F; they also visited the correct corner far less often than the sham-90 group, *U*(11, 10) = 17.00. It is apparent, therefore, that although lesioned animals were able to use some feature of the arena to navigate, they did so with great difficulty and at a much reduced accuracy relative to controls.

A t-test revealed that during the test trial carried out on session 21 in the rectangular pool, rats in the sham-90 group spent more time in the quadrants adjacent to corners A and C than those in the hippocampal-90 group, t(19) = 2.18. Rats in the sham-90 group spent a mean of 61.13 % of the trial swimming in these quadrants, compared to 54.51 % by the hippocampal-90 group. A one-sample t-test revealed that the performance of the hippocampal-90 group on this test trial was equivalent to chance, *t*(10) = 2.18. The sham-90 group, however, spent more time in the correct pair of quadrants than would be expected by chance, *t*(9) = 4.98. This group also made more choices to these corners during the subsequent two training sessions in the rectangle than the hippocampal-90 group, as shown in Figure 18. This difference was significant, *U*(11, 10) = 13.00. Although it is possible that the superior performance of

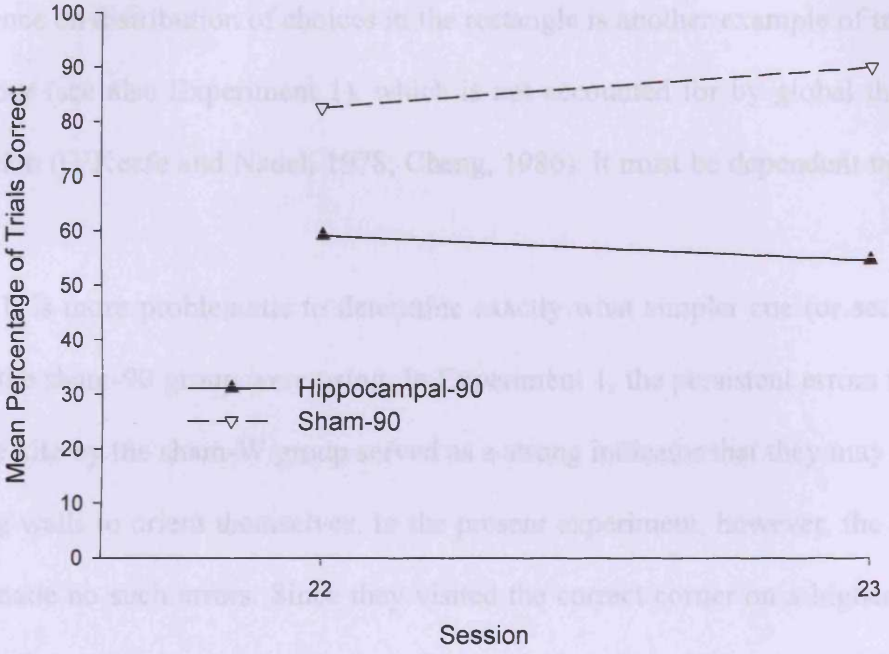

Figure 18. The distribution of choices for rats in the hippocampal-90 and sham-90 groups of Experiment 2, during sessions 22 and 23. These sessions were carried out in the rectangular pool.

the sham-90 group compared to the hippocampal-90 group in the rectangle is a result of rapid learning, it may also be a result of experience gained during training in the kite-shaped pool. In either case, the results of the probe trial indicate that training in the kite-shaped pool exerted a greater subsequent influence on behaviour in the rectangle for the sham rats than it did for the lesioned animals. The influence of prior experience on distribution of choices in the rectangle is another example of transfer of behaviour (see also Experiment 1), which is not accounted for by global theories of navigation (O'Keefe and Nadel, 1978; Cheng, 1986). It must be dependent upon local cues.

It is more problematic to determine exactly what simpler cue (or set of cues) rats in the sham-90 group were using. In Experiment 1, the persistent errors to corner F of the kite by the sham-W group served as a strong indicator that they may be using the long walls to orient themselves. In the present experiment, however, the sham-90 group made no such errors. Since they visited the correct corner on a higher number of trials than any other, they must have been able to use some feature which defined this correct corner unambiguously. There were features present in the kite-shaped arena that could provide such a reliable indicator but that are not present in the rectangle, such as the acute angle F and the obtuse angle H. Exclusive use of these cues can be ruled out, because if they were the critical features for orientation in the kite then we would not expect any transfer of behaviour to the novel rectangular arena where these features were absent, and such strategies were, presumably, redundant. Instead, there must be some feature present in both shapes which unambiguously defined the correct corner in the kite.

As an attempt to shed light on what that feature might be, I have divided the performance of the sham-90 group in the kite into two types of trials: those upon which they were released from one of the long walls, and those upon which they were released from a short wall. In every session, each rat was released from a long wall twice and a short wall twice. Over the last six sessions, correct initial choices were made on 42.50 % of trials when the rats were released from long walls, but 61.72 % of trials when they were released from the short walls. This difference is significant, *T*(8) = 4.00, and is consistent with the notion that these rats may have oriented themselves by using the shorter walls. If this was the case, this behaviour might be expected to have transferred well to the rectangular environment, in which these short walls were still present.

In order to explore this possibility, I have examined the performance of the sham-90 group when they were released from a short wall during training in the rectangle. If a rat swam to a corner in the rectangle which had the same geometric properties as the correct corner in the kite and was adjacent to the point at which the animal was released, it was referred to as the adjacent-correct (AC) corner. Similarly, the remaining corners were termed the opposite-correct (OC) corner, the adjacent-incorrect (AI) corner, and the opposite-incorrect (OI) corner. When released from one of the short walls, rats in the sham-90 group visited the AC corner first on 70 % of trials, the OC corner on 15 % of trials, the AI corner on 12.50 % and the OI corner on 2.50 % of trials. This distribution is different to that which would be expected by chance, Friedman $\chi^2(3, 10) = 17.36$. Crucially, the frequency of visits to corner AC was greater than to corner OC, *T*(10) = 4.00. When released from the long walls of the rectangle, rats in the sham-90 group visited the AC corner first on 57.50 % of trials, corner OC on 30 % of trials, AI on 10 % of trials and corner OI on 2.50% of trials. This distribution is different from chance, Friedman $\chi^2(3, 10) = 14.31$; however, the frequency of choices to the AC and OC corners was equivalent, *T*(8) = 7.50. In other words, rats demonstrated a preference for swimming to the adjacent rather than the opposite correct corner when released from the short sides of the rectangle, but not when they were released from the long sides. This finding suggests that, although rats in the sham-90 group acquired a preference for turning in a particular direction when released from a short wall, no such preference was acquired for turning in any particular direction when released from one of the long walls. Similar results were obtained by Pearce, Good, Jones, and McGregor (2004). Taken together with the analysis of choices during training in the kite presented above, this finding suggests that rats may have learned to orient in the kite by turning in a particular direction when released from a short wall. It must be stressed, though, that this analysis is somewhat speculative. Other local cues may have governed orientation in the kite and the subsequent preference shown during test trials in the rectangle, and the analysis presented here is primarily intended to illustrate the sort of local cues that rats may use. Another potential source of information is the spatial arrangement of walls at the correct corner; this type of strategy would permit rats to choose the correct corner over the incorrect corner in the kite, and would also allow such behaviour to transfer well to the rectangle. However, it is difficult to see how a strategy based on the spatial arrangement of walls at a corner should lead to rats choosing the adjacent correct corner more often when they are released from a short wall, but not when they are released from a long wall.

In contrast to the sham-90 group, the hippocampal-90 group did not show a preference for any particular corner when placed into the rectangle. They did, however, visit the correct right-angled corner more frequently than the incorrect right-angled corner in the kite. The most likely explanation for these findings is that the preference shown by the hippocampal-90 group in the kite was a result of learning based on some local cue which was not present in the rectangle. This rules out learning based on the spatial arrangement of walls at the correct corner. Two examples of cues which are present in the kite but not the rectangle are corners F and H. Rats in the hippocampal-F group learned to visit corner F more often than any other, a finding which suggests that rats in this group may have been able to orient by using corner F as a proximal local cue. Similarly, rats in the hippocampal-90 group may have visited the correct right-angled corner more often than the incorrect right-angled corner because they used corner F as a distal local cue. A strategy based on swimming away from this cue in a particular direction (left or right) would be capable of producing the kind of performance shown by the hippocampal-90 group.

In summary, the results of Experiment 2 show that rats with hippocampal lesions are able to use information provided by the walls of an all-white arena to orient under some circumstances. This was demonstrated by both the hippocampal-F group and the hippocampal-90 group, although rats in this latter group still showed a marked deficit when compared to controls. The pattern of corner choices made by the sham-90 group indicates that rats are able to learn to avoid corner F in the kite. Although it is possible that the sham-W group in Experiment 1 did not learn to avoid this corner because they were trained in the kite-shaped arena for fewer trials than in the present experiment, it also possible that it was a result of prior experience in the rectangle. The notion that learning based on local cues in one environment may influence behaviour in a subsequent environment is reinforced here, with the good performance observed in the sham-90 group during test trials in the rectangle.

EXPERIMENT 3

In Experiment 2, the hippocampal-90 group visited the correct right-angled corner more frequently than the incorrect right-angled corner in the kite. I suggested that this may be because these rats used a strategy based on some distal local cue, such as corner F (see Figure 3). In Experiment 3, this idea was tested with a novel distal cue. While rats in the hippocampal-90 group of Experiment 2 showed a preference for the correct right-angled corner over the incorrect right-angled corner, this preference was not as great as that displayed by the sham-90 group. Also, the lesioned rats made frequent errors by visiting corner F. Despite showing the appropriate preference for the correct right-angled corner, the hippocampal-90 group had some difficulty using a distal cue. In Experiment 3, rats were trained with a more explicit distal cue. A group of hippocampally lesioned rats (the hippocampal-BW group) and a group of control rats (the sham-BW group) were trained in a rectangular watermaze with three white (W) walls and one black (B) wall (Figure 19). Wall CD of the rectangle was black, and the platform was located in either corner A or corner B. In this arena, there were two ways in which the correct corner could be identified. The first was by reference to the information provided by the rectangular shape of the environment. The second was by the use of the black wall CD as a distal local cue. For an animal to learn to find the platform based only on this cue, it would have to learn in which direction it needed to turn and swim in relation to the black wall.

Based on Experiment 1, in which rats with hippocampal lesions had little difficulty using information provided by black walls in a rectangular arena, the information provided by the black wall here was expected to be an easier source of distal local information than corner F in the kite; as such the hippocampal-BW group

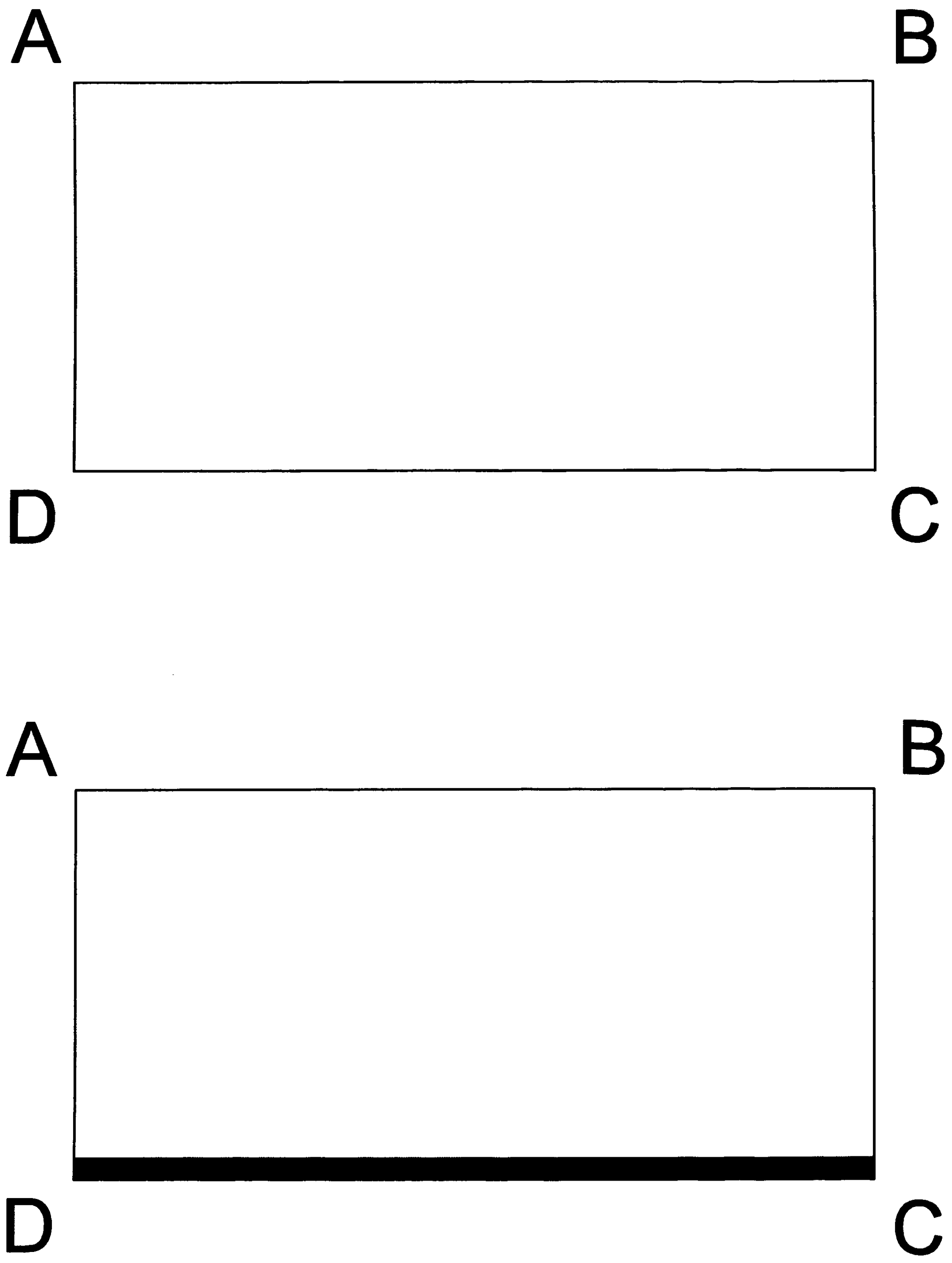

Figure 19. Schematic overhead views of the two test environments in which animals were trained during Experiment 3. The hippocampal-W and sham-W groups were trained in a rectangular environment with four white walls (top panel) and the hippocampal-BW and sham-BW groups were trained in an environment with two short white walls, one long white wall, and one long black wall (bottom panel). Wall CD in this latter environment was black.

here were expected to find the platform easily. To assess the use of the black wall, additional groups of rats (the hippocampal-W group and the sham-W group) were trained in an all-white rectangle. If the groups trained in the black and white rectangle perform more accurately than those trained in the all-white rectangle, we will be able to conclude that the black wall is a useful cue for navigation. Moreover, a preference for the correct white corner over the incorrect white corner in the hippocampal-BW group would suggest that lesioned rats are capable of using distal cue information to orient. This notion would be strongly supported if rats in the hippocampal-BW group more accurately discriminated between white corners than the hippocampal-W group.

An additional purpose of Experiment 3 was to assess the ability of rats with hippocampal lesions to discriminate between the two ends of a white wall. In Experiment 1, the hippocampal-W group failed to search at the correct ends of the long walls any more often than the incorrect ends; in other words, they failed to discriminate between the correct and incorrect corners. If controls oriented by selecting a single wall and turning in a particular direction to it, then it may be reasonable to assume that rats with hippocampal lesions are impaired because they cannot do so. Thus far, I have little evidence that rats with hippocampal lesions are able to learn to swim to the left rather than the right, or vice versa. That the hippocampal-BW group of Experiment 1 visited the correct corner more than the incorrect corner may simply have been a result of additional black and white cues created at each corner, where a black and white wall met. In Experiment 3 no such cues were present in corners A and B, and rats in the hippocampal-BW group could only learn to visit the correct white corner more often than the incorrect white corner by orienting in a particular direction from the opposite black wall CD.

Method

Subjects and apparatus. The subjects were 32 male rats from the same stock and housed in the same manner as for Experiment 1. Prior to surgery, all animals weighed between 300 and 350 g. At the outset of the experiment, the rats were assigned to four groups, each containing eight rats. The rectangular arenas were composed of the same walls as those used in Experiment 1; four white walls were used to construct the white rectangle, and two short white walls, one long white wall, and one long black wall were used to construct the black and white rectangle. In this rectangle, wall CD was black. The platform was always located in corner A or corner B.

Procedure. Rats were transported to the room adjacent to the test room in groups of four. All rats received four sessions of pre-training in the circular pool, in the same manner as for previous experiments. In the following stage, all sessions again consisted of four trials. Rats were released into the rectangular arena and allowed up to 90 s to locate the platform with the beacon attached to it during sessions 5-8 only. Rats were released from the mid-points of the four walls, facing the wall and with the four release points selected in a random order. During training sessions in the rectangle, the platform was located consistently for each rat. For half the rats in the hippocampal-W and sham-W groups, the platform was located in either corner A or corner C; for the other half, it was located in either corner B or corner D. For half the rats in the hippocampal-BW and sham-BW groups, the platform was located in corner A, and for the remainder it was located in corner B. The centre of the platform was 25 cm from the corner, along a notional line that bisected the corner. The platform was located in these positions for a total of 16 sessions.

Session 21 consisted of three training trials of the type described above, and one test trial. This test trial was conducted with the platform removed from the pool, in the same rectangular arena for each rat as the previous training trials. In the case of test trials conducted in the white rectangle, the percentages of time spent in the two quadrants adjacent to correct corners were combined. In the case of the black and white rectangle, the amount of time spent in the quadrant in which the platform had previously been located was divided by the amount of time spent in the quadrants adjacent to the two white corners combined; in this way, scores for each group reflect the proportion of time spent in featurally correct quadrants that was spent in corners which were also correct with respect to the shape of the environment. Session 22 was conducted with the hippocampal-BW and sham-BW groups only. They were given one test trial in the all-white pool.

All procedural details that have been omitted were the same as for Experiment 1.

Results

Figure 20 shows reconstructions of the maximum (light shading) and minimum (dark shading) extent of the hippocampal lesions on a series of horizontal sections taken at distances in mm ventral to the surface of the brain (top to bottom: -3.1, -3.6, -4.6, -5.6, -6.6, -7.6, -8.4 mm). Two rats in the hippocampal-BW group sustained extensive damage to the temporal cortex and were therefore excluded from the analyses, leaving six rats in this group. All remaining rats with hippocampal lesions sustained damage to the dentate gyrus and CA subfields at all levels, and

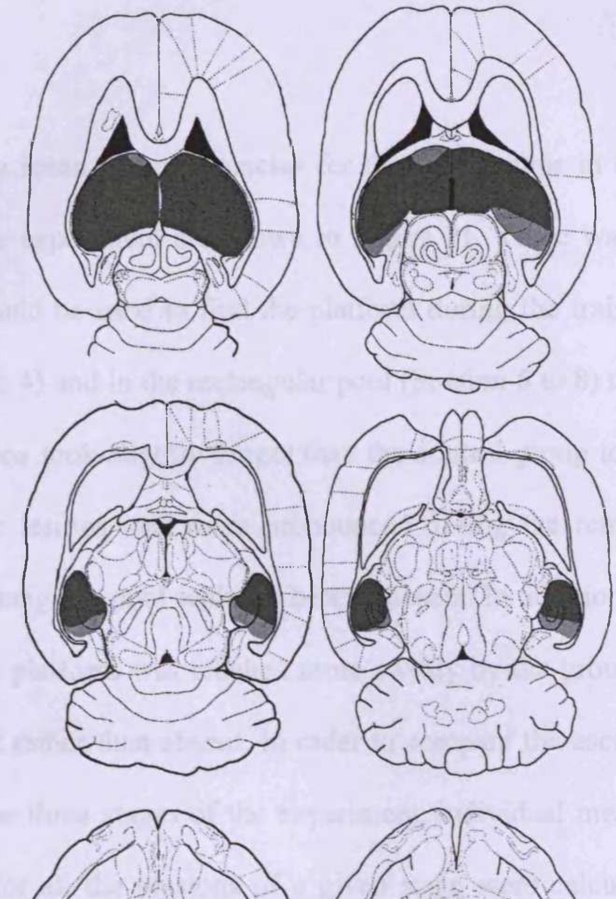

Figure 20. The maximum (light shading) and minimum (dark shading) extent of the hippocampal lesions for Experiment 3.

experienced cell loss of 70 % - 100 %. These rats also sustained damage to the ventral subiculum.

Latencies. The mean escape latencies for the four groups in each session of the three stages of the experiment are shown in Figure 21. There was a suggestion that when a beacon could be used to find the platform during the training in the circular pool (Sessions 1 to 4) and in the rectangular pool (Session 5 to 8) that the groups with hippocampal lesions took slightly longer than the control group to find the platform. This effect of the lesions was more pronounced during the remaining sessions of training in the rectangular pool with the beacon absent. In addition, it is evident from Figure 21 that the platform was reached more swiftly by the groups trained with the black wall present rather than absent. In order to compare the escape latencies of the four groups for the three stages of the experiment, individual mean escape latencies for each subject for all the sessions of a given stage were calculated. A three-way ANOVA was performed using experimental stage (pre-training, training in the rectangle with the beacon attached, and training in the rectangle with the beacon removed), context (white rectangle or black and white rectangle) and lesion (hippocampal or sham) as factors. There was a significant effect of stage, $F(2, 52) = 114.77$; of lesion, $F(1, 26) = 76.46$; and a significant interaction between the two, $F(2, 52) = 19.12$. There was no effect of training context, $F(1, 26) = 2.85$, although the Context × Stage interaction was significant, $F(2, 52) = 8.37$. The remaining interactions were not significant: Context × Lesion, $F < 1$; and Context × Lesion × Stage, $F(2, 52) = 1.53$. Tests of simple main effects were conducted to explore the Stage × Lesion interaction. The escape latencies for the two groups with hippocampal lesions combined were significantly slower than for the two control

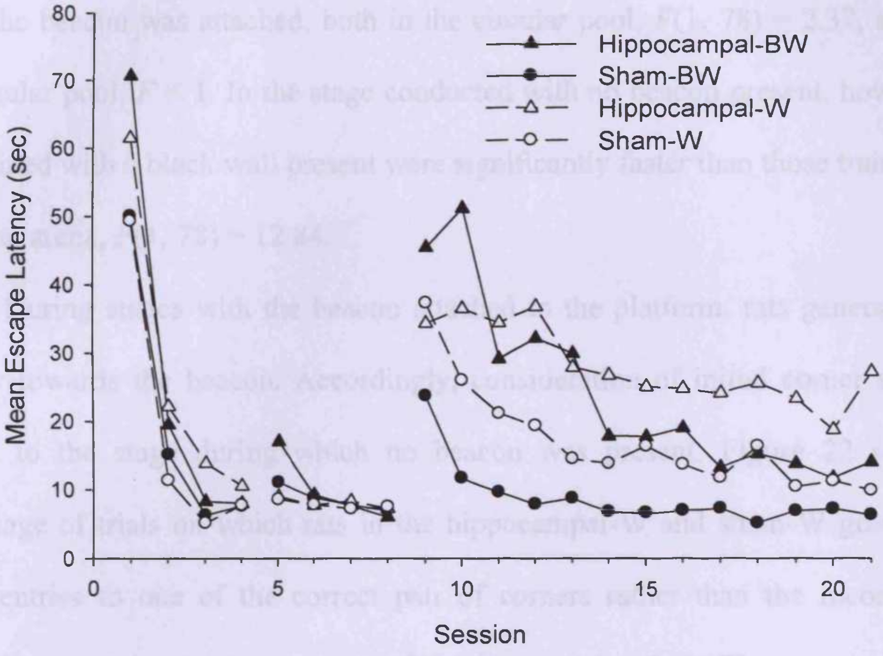

Figure 21. Mean escape latencies for the four groups of Experiment 3. Sessions 1-4 were conducted in the circular pool with the beacon attached to the platform, sessions 5-8 were conducted in the rectangular pool with the beacon attached, and sessions 9-21 were in the rectangular pool with the beacon removed.

groups combined during the first, $F(1, 78) = 29.92$, and the final stage of the experiment, $F(1, 78) = 85.73$, but not for the second stage, $F < 1$. Additional simple main effects tests were conducted to investigate the significant Context × Stage interaction. Rats trained in the two contexts were equally quick to find the platform when the beacon was attached, both in the circular pool, $F(1, 78) = 2.37$, and in the rectangular pool, $F < 1$. In the stage conducted with no beacon present, however, the rats trained with a black wall present were significantly faster than those trained in the all-white arena, $F(1, 78) = 12.84$.

During stages with the beacon attached to the platform, rats generally swam directly towards the beacon. Accordingly, consideration of initial corner choices is limited to the stage during which no beacon was present. Figure 22 shows the percentage of trials on which rats in the hippocampal-W and sham-W groups made initial entries to one of the correct pair of corners rather than the incorrect pair. Throughout training in the absence of the beacon, the sham-W group made initial choices to correct corners on a higher proportion of trials than the hippocampal-W group. In order to compare the asymptotic performance of the two groups the mean percentage of trials on which individual rats headed directly for a correct corner during the final six sessions of training was calculated. Analysis of these scores revealed that the hippocampal-W group headed directly for a correct corner significantly less frequently than the sham-W group, $U(8, 8) = 6.5$. Despite this, the lesioned animals entered a correct corner on 65 % of trials during the last six sessions. A binomial test revealed that this was a greater proportion of trials than would be expected by chance.

For the two groups trained in the white rectangle, there were only two types of corner – correct and incorrect. In contrast, the performance for the remaining two

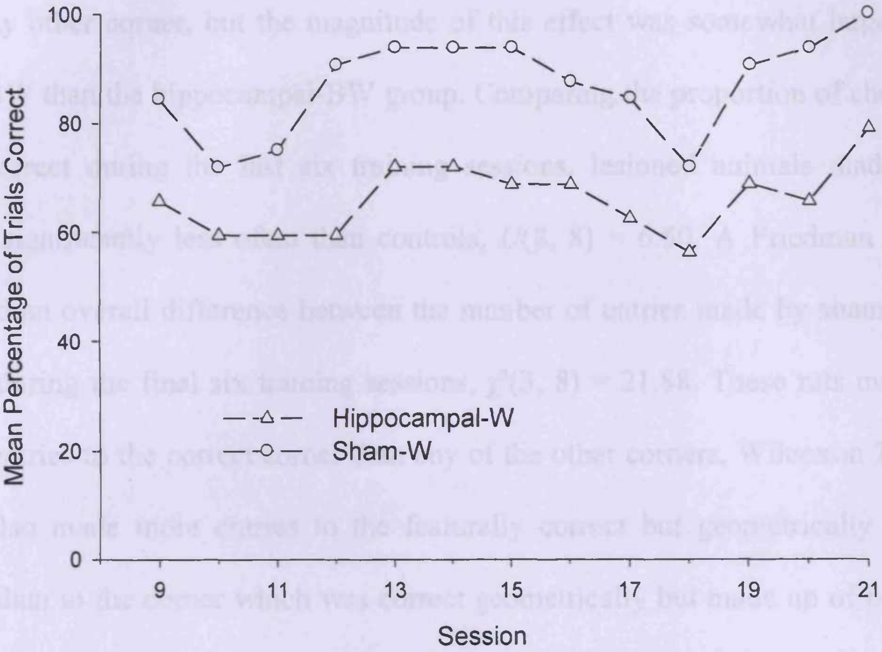

Figure 22. The mean percentage of trials on which the hippocampal-W and sham-W groups entered a correct corner before an incorrect corner during each session in the rectangle in Experiment 3.

groups can be analysed in terms of the percentages of trials on which they entered each of the four corners of the pool. Figure 23 shows these results for the sham-BW group and Figure 24 shows the results for the hippocampal-BW group. Both groups swam directly to the corner containing the platform on considerably more occasions than any other corner, but the magnitude of this effect was somewhat larger for the sham-BW than the hippocampal-BW group. Comparing the proportion of choices that were correct during the last six training sessions, lesioned animals made correct entries significantly less often than controls, *U*(8, 8) = 6.50. A Friedman ANOVA revealed an overall difference between the number of entries made by shams to each corner during the final six training sessions, $\chi^2(3, 8) = 21.88$. These rats made more initial entries to the correct corner than any of the other corners, Wilcoxon *T*s(8) = 0. They also made more entries to the featurally correct but geometrically incorrect corner than to the corner which was correct geometrically but made up of both black and white walls, *T*(8) = 0. The number of first entries to the geometrically incorrect white corner and the corner which was incorrect both geometrically and featurally was equivalent, *T*(8) = 4.50; as was the number of visits made to the two black and white corners, *T*(3) = 0. There was also an overall difference between the number of choices made to each corner for the hippocampal-BW group, Friedman $\chi^2(3, 6) = 9.44$. They made more entries to the correct corner than either the geometrically incorrect white corner, *T*(6) = 0; and the corner which was incorrect both featurally and geometrically, *T*(6) = 0. The remaining pair wise comparisons revealed no differences: the incorrect white corner vs. the geometrically correct black and white corner, *T*(5) = 6.00; the two geometrically incorrect corners, *T*(4) = 3.50; the two geometrically correct corners, *T*(6) = 1.00; and the two black and white corners, *T*(5) = 5.00.

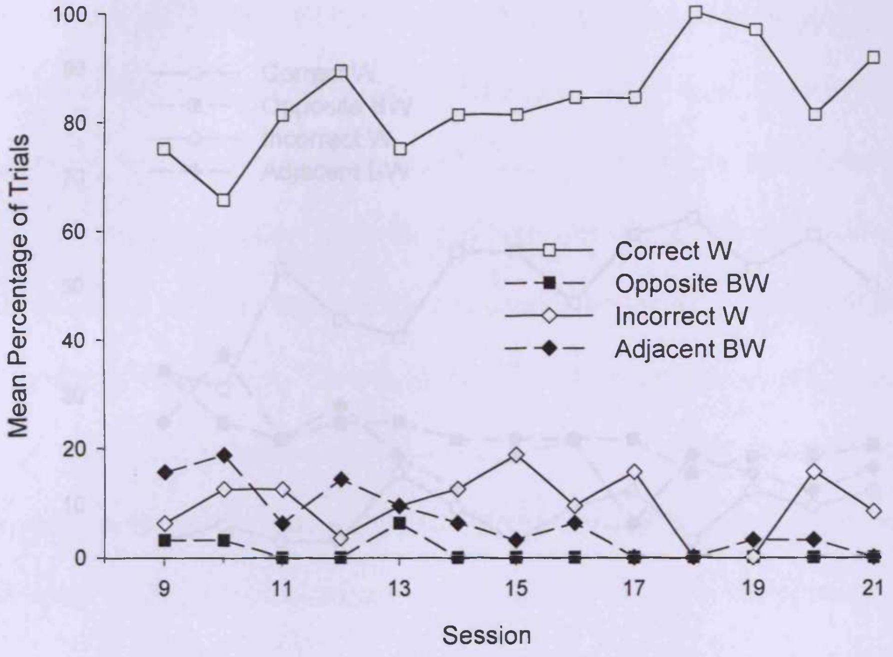

Figure 23. The distribution of choices during training for rats in the sham-BW group of Experiment 3. Correct W = the corner containing the platform; Opposite BW = the corner opposite the correct corner; Incorrect W = the corner located along a long wall from the correct corner; Adjacent BW; the corner located along a short wall from the correct corner.

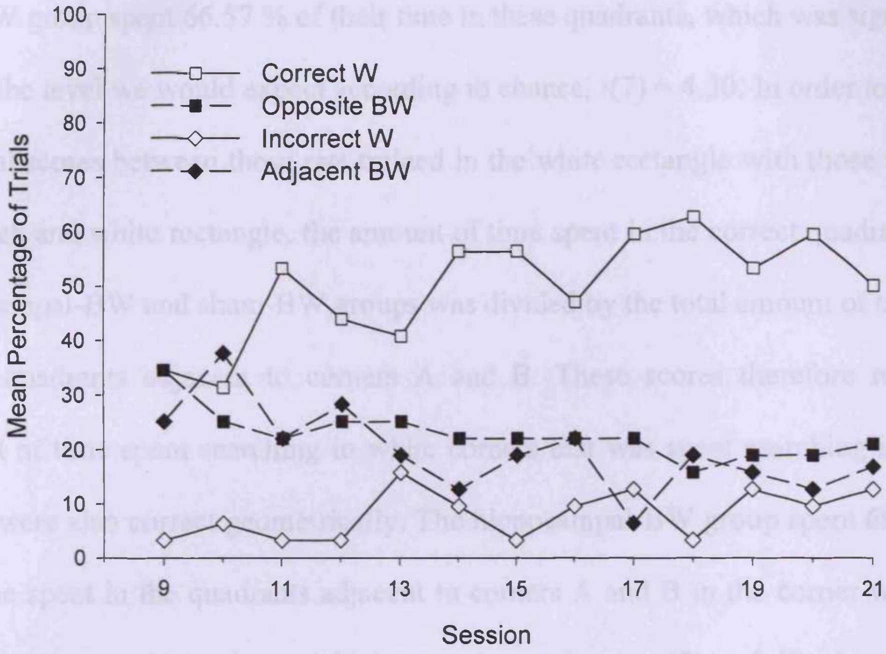

Figure 24. The distribution of choices during training for rats in the hippocampal-BW group of Experiment 3. Correct W = the corner containing the platform; Opposite BW = the corner opposite the correct corner; Incorrect W = the corner located along a long wall from the correct corner; Adjacent BW; the corner located along a short wall from the correct corner.

During the test trial of session 21, a record was taken of the amount of time spent in different areas of the pool. The hippocampal-W group spent a mean of 54.25 % of the trial swimming in quadrants that were correct with respect to the rectangular shape of the pool. This was equivalent to chance performance, $t(7) = 1.50$. Rats in the sham-W group spent 66.57 % of their time in these quadrants, which was significantly above the level we would expect according to chance, $t(7) = 4.30$. In order to compare test trial scores between those rats trained in the white rectangle with those trained in the black and white rectangle, the amount of time spent in the correct quadrant by the hippocampal-BW and sham-BW groups was divided by the total amount of time spent in the quadrants adjacent to corners A and B. These scores therefore reflect the amount of time spent searching in white corners that was spent searching in corners which were also correct geometrically. The hippocampal-BW group spent 69.30 % of the time spent in the quadrants adjacent to corners A and B in the corner which was correct with respect to shape, which was above chance, $t(5) = 4.48$; the sham-BW group scored 84.27 %, which was also above chance, $t(7) = 8.14$. A two-way ANOVA of the scores for all four groups revealed an effect of context, $F(1, 26) = 12.64$; an effect of lesion, $F(1, 26) = 18.21$; and no significant interaction between the two, $F < 1$. Rats more effectively distinguished between white corners when they had received sham lesions than hippocampal lesions, and when there was a black wall present. That the hippocampal-BW group visited the geometrically correct white corner more often than the geometrically incorrect white corner likely reflects the use of the black wall to orient. These rats made effective use of a distal local cue for finding the platform. An alternative account is that the presence of the black wall somehow enabled rats in the hippocampal-BW group to distinguish the correct from the incorrect white corner on the basis of their geometric properties. This account seems unlikely. During the test trial of session 22, conducted in a white rectangle, the hippocampal-BW group spent an average of 51.46 % of the trial swimming in quadrants near corners which were correct with respect to shape, whereas the sham-BW group scored 62.10 %. This difference is significant, *t*(12) = 4.01. The performance of the hippocampal-BW on this test trial is no different from chance, *t*(5) < 1. The hippocampal-BW group were unable to use information provided by the shape of the environment, so it seems more credible that the good performance by this group in the previous stage was a consequence of the black wall being used as a polarising cue.

During training, rats in the hippocampal-BW group visited the correct corner and the geometrically equivalent corner opposite on a statistically equivalent number of occasions, although a numerical difference was apparent. It seems surprising that these rats would fail to discriminate between these two corners, since the correct corner was composed of two white walls while the opposite corner was bounded by the long black wall CD. That there is no statistical difference between the two is likely attributable to an insensitivity of the test; this is made more credible by the results of the test trial conducted with the black wall present, in which rats in the hippocampal group spent more time swimming in the quadrant near the correct corner than the one opposite, *t*(5) = 3.61. Although rats in the hippocampal-BW group visited the correct white corner more than the incorrect white corner, their performance was not as good as that seen in the sham-BW group. A likely explanation is that the lesioned animals were able to orient only by use of the black wall, whereas controls were able to use both the black wall and the information provided by the shape of the rectangle. This argument is similar to that used to explain the difference in performance between the hippocampal-BW and sham-BW groups of Experiment 1.

One interesting finding in this experiment is that the hippocampal-W group made more choices to correct corners during acquisition than we might expect by chance. The reasons for this are unclear; this result is contrary to the findings from the hippocampal-W group of Experiment 1. Furthermore, the hippocampal-W group in the current experiment spent no more time searching near to the correct than the incorrect corners during a test trial in the white rectangle. Whatever the reason for the good performance of the hippocampal-W group during acquisition here, the weight of evidence suggests that rats with hippocampal lesions have great difficulty in using information provided by the rectangular shape of an arena, and are severely impaired in relation to controls.

In summary, then, hippocampectomized rats had difficulty using information provided by shape to identify the correct corner, but were able to use the local feature information provided by the black wall with ease. This is consistent with the findings of Experiment 1, although in that experiment the local information was close to the platform and the feature information was further away here. These results therefore extend the generality of the findings of Experiment 1. From the current results, it is apparent that rats with hippocampal lesions are able to use distal cue information to orient, as well as being able to turn in a particular direction in relation to that cue.

EXPERIMENT 4

The evidence presented so far shows that rats with hippocampal lesions are able to find a platform accurately in one corner of a rectangular arena when there is feature information available, but not when discrimination of the corners must be carried out according to geometric cues alone. Although a traditional explanation (O'Keefe and Nadel, 1978; Cheng, 1986) for this might be that rats with hippocampal lesions are impaired at using geometric cues because they lack a global representation of the shape of the environment, the results of transfer tests carried out as part of Experiments 1 and 2 suggest that animals are able to navigate in distinctively-shaped environments by referring to local rather than global cues. We can therefore suppose that one reason for the poor performance of the hippocampally-lesioned animals is that they are not able to effectively use the local cues which control animals take advantage of to navigate in the featureless arenas.

Results from the transfer test carried out in Experiment 1 give some insight into what those local cues might be when rats are trained in a featureless rectangular environment. The distribution of choices when the sham-W group were placed into the kite was most consistent with the idea that they had used the long walls to orient in the rectangle. The deficit seen in the hippocampal-W groups, then, may be a result of their poor capacity to use the long walls of the rectangle to orient.

Hippocampal rats are not impaired, however, in using some other local cues. The hippocampal-BW group of Experiment 1 accurately discriminated between the two correct corners and the two incorrect corners, and their behaviour when subsequently placed into the black and white kite-shaped arena suggested that they had oriented in the rectangle by using the long black walls. These results show that, although they were not able to select and orient by walls according to length information, they were able to orient by walls according to colour information.

Why should rats with hippocampal lesions be able to use information about the colour of the walls but unable to use their lengths to discriminate between corners? In order to use a cue for navigation, an animal must be able to select that cue over any other, a prerequisite for which is the ability to tell the available cues apart. It is possible that the failure of rats with hippocampal lesions to orient according to the long walls of the environment reflects an inability to identify the long walls – to distinguish the long from the short walls of the arena. This possibility was explored in Experiment 4.

Rats were trained to find a platform near to the mid-point of one of the long walls of a rectangular arena. In order to accurately choose the long walls over the short walls, rats must be able to distinguish between the two. Prior to this experiment, a preliminary study was carried out in which unoperated rats were trained to find a hidden platform close to the mid-point of either the long or the short walls. During this preliminary study, performance was assessed by noting whether rats went to the long or the short walls first upon release into the pool. For this purpose, choice zones were superimposed onto the pool at the mid-points of each of the four walls of the rectangle (Figure 25). For those rats trained with the platform close to the long walls, performance was good – the first choice zone entered after release was usually one of the zones near to a long wall. For rats trained with the platform close to the short walls, however, the percentage of trials on which they entered a correct zone before an incorrect zone was much lower. They frequently entered an incorrect zone close to a long wall before a correct zone close to a short wall. Informal observation of these animals suggested that this may have been because the shape of the pool meant that

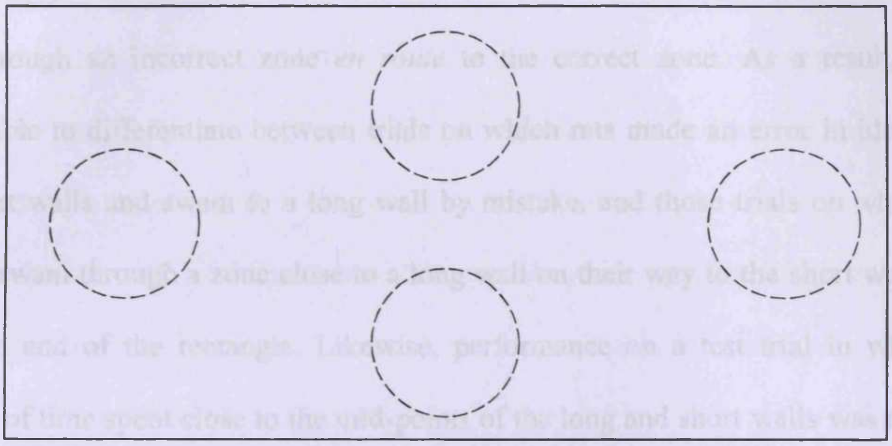

Figure 25. Schematic representation of a rectangular test environment, with the choice zones used in Experiment 4 superimposed. The platform was located 25 cm from the mid-point of one of the long walls, and a choice was considered to have been made when a rat's head entered a circular zone of 30 cm diameter centred on either the centre of the platform or an equivalent position near to any of the other three walls. These choice zones are shown by broken lines.

the zones close to the long walls were relatively near to one another, and there was little scope for rats to swim from one end of the pool to the other without passing through one of these two areas. If a rat was released from the south end of the pool, for instance, and swam towards the short wall at the north end, it would almost always pass through an incorrect zone *en route* to the correct zone. As a result, it was impossible to differentiate between trials on which rats made an error in identifying the short walls and swam to a long wall by mistake, and those trials on which they simply swam through a zone close to a long wall on their way to the short wall at the opposite end of the rectangle. Likewise, performance on a test trial in which the amount of time spent close to the mid-points of the long and short walls was recorded was difficult to assess because a rat swimming from one short wall to the other almost always passed through the area close to the mid-points of the long walls. For these reasons, no rats in Experiment 4 were trained to find a platform near to the short walls of the rectangle; the long walls were used exclusively.

Two groups were trained to find a platform close to the mid-point of a long wall in a white (W) rectangle, the hippocampal-W and sham-W groups. Additional groups (the hippocampal-BW and sham-BW groups) were trained in a similar way, except that the short walls of the rectangle were coloured black (B). These groups were able to locate the platform by choosing white walls over black walls; they did not need to learn anything about the lengths of the walls of the environment. If the hippocampal-BW and sham-BW groups perform comparably, it will support the notion that any impairment seen in the white rectangle is due to a deficit in using length information.

Performance was assessed by measuring choices, using circular zones centred on the location of the platform and equivalent locations close to the other walls.

Additionally, performance following acquisition was assessed by a series of test trials, during which rats were allowed to swim freely in the absence of a platform. For the first test trial, each rat was tested in its training environment. Subsequent test trials were aimed at separating the use of features and geometric cues by rats trained in the black and white pool. One test involved placing all rats into a white rectangle, in order to compare the degree to which rats trained in the black and white pool were able to use length information with those trained in the white arena. Subsequent test trials were conducted with the hippocampal-BW and sham-BW groups only, placing them into a black and white square to assess their use of feature information when length information was removed.

Method

Subjects and apparatus. The subjects were 45 male rats from the same stock and housed in the same manner as for previous experiments. Prior to surgery, all animals weighed between 300 and 350 g. At the outset of the experiment, the rats were assigned to four groups; the hippocampal-W group contained 13 rats, the hippocampal-BW group contained 12 rats, and the sham-W and sham-BW groups each contained 10 rats. Rats in the hippocampal-W and hippocampal-BW groups were given hippocampal lesions and rats in the sham-W and sham-BW groups were subjected to a sham operation, in the same way as for previous experiments.

The rectangle was constructed in a similar way to previous experiments, with two long white walls and two short walls which were either black or white. In this experiment, a square arena was also used. The walls of the square each measured 1.4 m, and each was either white or black. The square was made up of two white and two black walls, with opposite walls matching. Rats in the hippocampal-W and sham-W groups were trained in the white rectangle, while those in the hippocampal-BW and sham-BW groups were trained in the black and white rectangle.

Procedure. Rats were transported to the room adjacent to the test room in groups of five, six, or seven. All rats received five sessions of pre-training in the circular pool, in the same manner as for previous experiments. There were then 20 training sessions in the rectangle, and all sessions again consisted of four trials. Rats were released into the rectangular arena and allowed up to 60 s to locate the platform with the beacon attached to it during sessions 6-10 only. Rats were released from the four corners of the rectangle, facing the corner and with the four release points selected in a random order. During training sessions in the rectangle, the platform was always located near to the mid-point of one of the long walls; the centre of the platform was 25 cm from the mid-point of the wall, along a notional line that was perpendicular to the plane of the wall.

Session 26 consisted of three training trials of the type described above, and one test trial. This test trial was conducted with the platform removed from the pool, in the same rectangular arena for each rat as the previous training trials. The percentage of time spent in a circular zone with a diameter of 15 cm centred on the platform's former location was measured, in addition to the amount of time spent in equivalent dummy zones close to the other walls of the rectangle. All rats were trained on session 27 in a similar way as for sessions 6-20. On day 28, rats were given three training trials and a test trial; the test trial was identical to that carried out on session 26, except that all rats were tested in the white rectangle.

The hippocampal-BW and sham-BW groups were trained in the black and white rectangle on session 29, and given three training trials and a test trial on session 30. This test trial was conducted in the black and white square. Sessions 31 and 32 consisted of one test trial each, both in the black and white square with the hippocampal-BW and sham-BW groups only.

All procedural details that have been omitted were the same as for previous experiments.

Results

Figure 26 shows reconstructions of the maximum (light shading) and minimum (dark shading) extent of the hippocampal lesions on a series of horizontal sections taken at distances in mm ventral to the surface of the brain (top to bottom: -3.1, -3.6, -4.6, -5.6, -6.6, -7.6, -8.4 mm). All rats sustained extensive damage to the hippocampus. For 19 rats, this damage was between 65 % and 100%; for the remaining 6 rats, cell loss was less than 50 %. These rats were excluded from the following analyses. Four of the excluded rats were from the hippocampal-W group, and two were from the hippocampal-BW group. In the following analyses, then, the hippocampal-W group contained nine rats and the hippocampal-BW group contained ten rats.

Mean latencies for each session of the experiment are shown in Figure 27. For each experimental stage, a mean latency was calculated for each animal and these scores were entered into a three-way ANOVA. For this analysis, latencies from sessions 29 and 30 were excluded because only the hippocampal-BW and sham-BW groups took part in those sessions. The analysis revealed that there was no overall

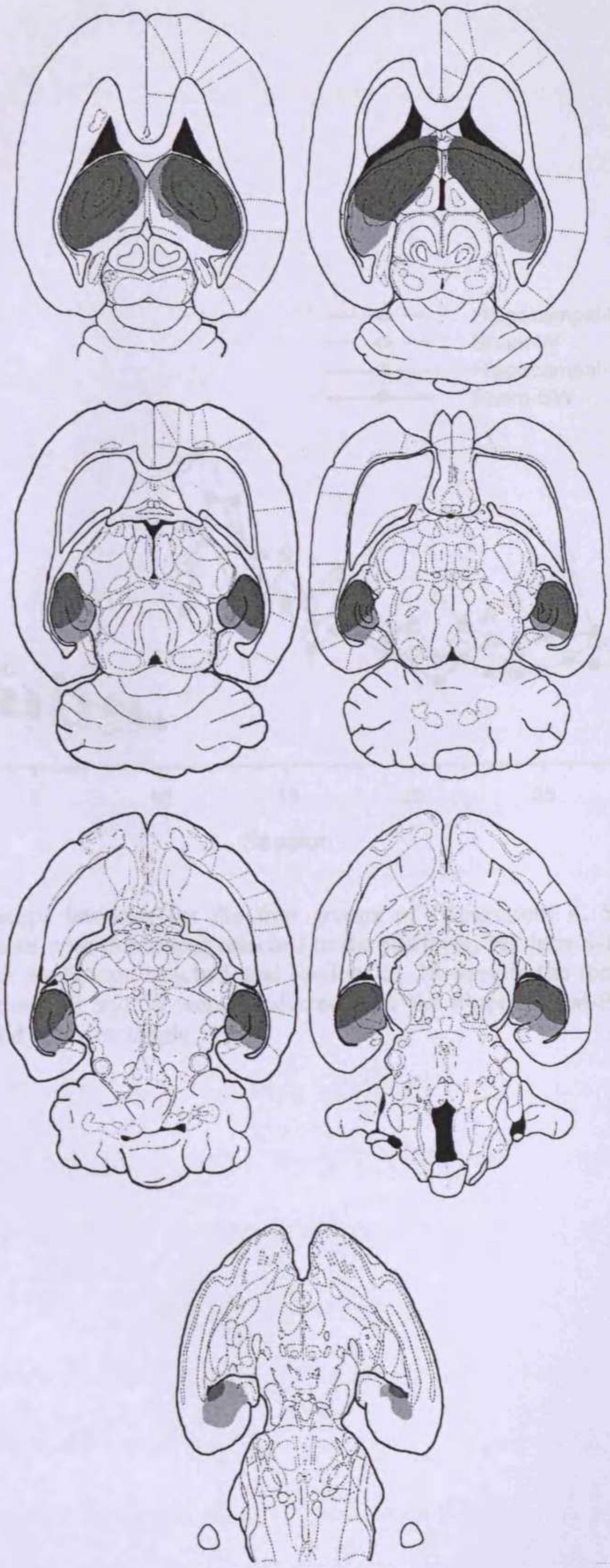

Figure 26. The maximum (light shading) and minimum (dark shading) extent of the hippocampal lesions for Experiment 4.

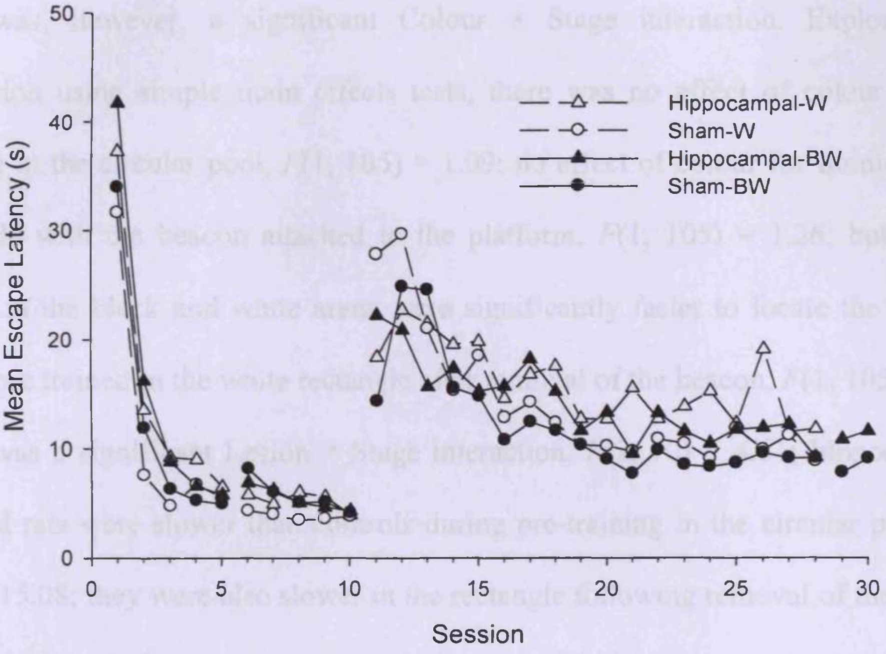

Figure 20. Mean escape latencies for the four groups of Experiment 4. Sessions 1-5 were conducted in the circular pool with the beacon attached to the platform, sessions 6-10 were conducted in the rectangular pool with the beacon attached, and sessions 11-28 were in the rectangular pool with the beacon removed. Sessions 29 and 30 were conducted with the hippocampal-BW and sham-BW groups only, in the black and white rectangle.

difference between those trained in the black and white arena and those trained in the white rectangle, $F(1, 35) < 1$; hippocampally lesioned rats were significantly slower than shams, $F(1, 35) = 7.94$; and there was a difference between the three stages of the experiment, $F(2, 70) = 207.38$. There was no Lesion × Colour interaction, $F < 1$; there was, however, a significant Colour × Stage interaction. Exploring this interaction using simple main effects tests, there was no effect of colour for pre-training in the circular pool, $F(1, 105) = 1.09$; no effect of colour for training in the rectangle with the beacon attached to the platform, $F(1, 105) = 1.26$; but the rats trained in the black and white arena were significantly faster to locate the platform than those trained in the white rectangle after removal of the beacon, $F(1, 105) = 4.11$. There was a significant Lesion × Stage interaction, $F(2, 70) = 4.61$; hippocampally lesioned rats were slower than controls during pre-training in the circular pool, $F(1, 105) = 15.08$; they were also slower in the rectangle following removal of the beacon, $F(1, 105) = 4.48$. There was no difference between lesioned rats and controls during training in the rectangle with the beacon present, $F < 1$. There was no Lesion × Colour × Stage interaction, $F < 1$.

For sessions 29 and 30, a mean latency across the two sessions was calculated for each rat in the hippocampal-BW and sham-BW groups. A between-subjects t-test revealed that the hippocampal-BW group were slower during these two sessions than the sham-BW group, $t(18) = 2.33$. In summary then, lesioned rats were slower than controls for all stages except training in the rectangle with the beacon present, and rats trained in the black and white rectangle took less time to find the platform than those trained in the white arena following removal of the beacon only.

Mean correct choices for each session are shown in Figure 28. For each rat, a mean number of trials correct during the final six training sessions (i.e. sessions 20-

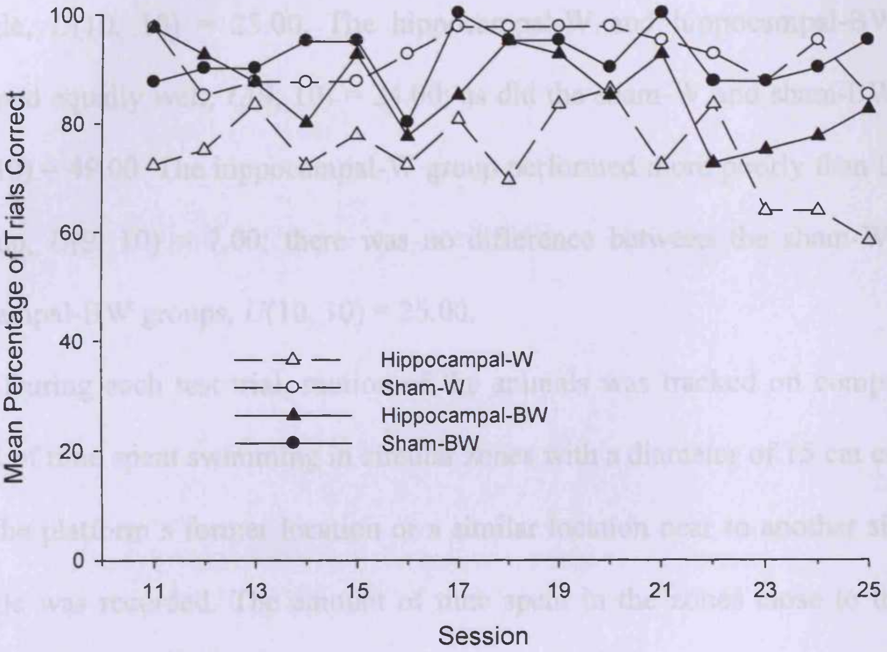

Figure 28. The mean percentage of trials on which the four groups entered a circular zone near the mid-point of a long wall before a short wall during sessions 11-25 in the rectangle in Experiment 4.

25) was calculated. There was an overall difference between the scores for the four groups, Kruskal-Wallis H(3, 39) = 15.53. The hippocampal-W group chose a correct zone before an incorrect zone less often than the sham-W group, *U*(9, 10) = 6.50; lesioned rats also performed more poorly than controls in the black and white rectangle, *U*(10, 10) = 23.00. The hippocampal-W and hippocampal-BW groups performed equally well, *U*(9, 10) = 24.00; as did the sham-W and sham-BW groups, *U*(10, 10) = 49.00. The hippocampal-W group performed more poorly than the sham-W group, *U*(9, 10) = 7.00; there was no difference between the sham-W and the hippocampal-BW groups, *U*(10, 10) = 25.00.

During each test trial, motion of the animals was tracked on computer. The amount of time spent swimming in circular zones with a diameter of 15 cm centred on either the platform's former location or a similar location near to another side of the rectangle was recorded. The amount of time spent in the zones close to the longer sides of the rectangle was combined for each animal, as was the amount of time spent in the zones close to the short sides. Scores for each test trial were entered into an ANOVA.

The percentage of the first test trial that was spent in zones near to the long and short walls for each group is shown in Figure 29. Rats in the hippocampal-W group spent the least time in the zones close to the long walls (20.79 %), whereas the sham-BW group spent the most time in these zones at 37.50 %. The highest amount of time spent in the zones close to the short walls was for the hippocampal-W group, and was 2.67 %. For this trial, there was a significant effect of lesion, *F*(1, 35) = 19.36; a significant effect of colour, *F*(1, 35) = 15.35; and a significant difference between the amount of time spent in the zones close to the long and short walls, *F*(1, 35) = 642.82. There was no Lesion × Colour interaction, *F*(1, 35) = 3.05; but there

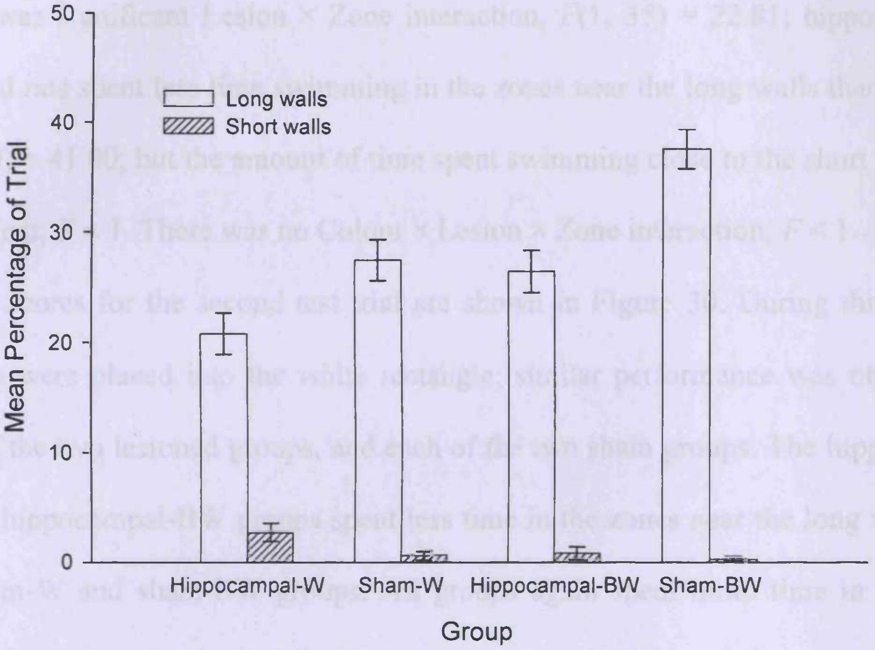

Figure 29. The mean percentage of the test trial carried out during session 26 that was spent in two 15 cm zones near the mid-points of the long walls, and the amount of time that was spent in equivalent zones near the short walls. Each group was tested in the same arena in which they had been trained. Error bars represent ± 1 standard error.

was a significant Colour × Zone interaction, *F*(1, 35) = 17.71. Rats trained in the black and white rectangle spent more time searching in the zones close to the long walls than those trained in the white arena, *F*(1, 70) = 32.90; but there was no effect of colour on the amount of time spent in the zones close to the short walls, *F* < 1. There was significant Lesion × Zone interaction, *F*(1, 35) = 22.81; hippocampally-lesioned rats spent less time swimming in the zones near the long walls than controls, *F*(1, 70) = 41.00; but the amount of time spent swimming close to the short walls was equivalent, *F* < 1. There was no Colour × Lesion × Zone interaction, *F* < 1.

Scores for the second test trial are shown in Figure 30. During this trial, all animals were placed into the white rectangle; similar performance was observed in each of the two lesioned groups, and each of the two sham groups. The hippocampal-W and hippocampal-BW groups spent less time in the zones near the long walls than the sham-W and sham-BW groups. All groups again spent more time in the zones near the long than the short walls. There was no overall difference between the groups trained in the two rectangles, *F*(1, 35) = 1.36. There was a significant effect of lesion, *F*(1, 35) = 10.30; and a difference between the amount of time spent in the zones near to the long and short walls, *F*(1, 35) = 421.66. There was no Colour × Lesion interaction, *F*(1, 35) = 1.45; nor was there a Colour × Zone interaction, *F*(1, 35) = 3.20. There was, however, a Lesion × Zone interaction, *F*(1, 35) = 16.92; the results here were similar to those from the first test trial. Hippocampally-lesioned rats spent less time in the zones close to the long walls than controls, *F*(1, 70) = 26.92; but they spent an equivalent amount of time in the zones close to the short walls, *F*(1, 70) = 3.19. There was no Colour × Lesion × Zone interaction.

The final three test sessions were conducted in the black and white square, with only the hippocampal-BW and sham-BW groups taking part. The mean

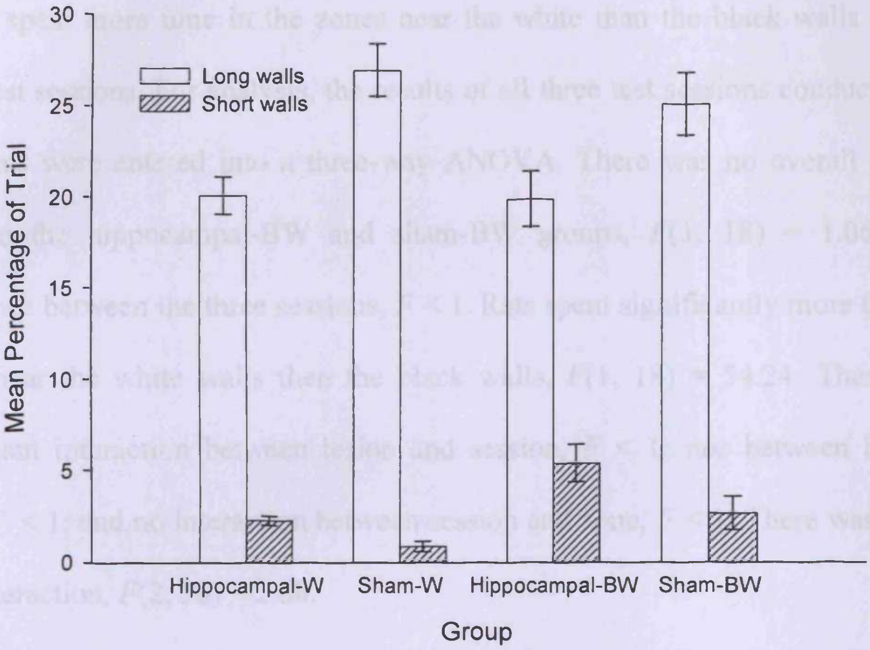

Figure 30. The mean percentage of the test trial carried out during session 28 that was spent in two 15 cm zones near the mid-points of the long walls, and the amount of time that was spent in equivalent zones near the short walls. Each group was tested in the white rectangle. Error bars represent ± 1 standard error.

percentage of these test trials which was spent in zones near to the black and white walls for each group is shown in Figure 31. Rats in the sham-BW group spent slightly more time in the zones near the white walls then the hippocampal-BW group during the first two of these test sessions, but this trend was reversed during the third. Both groups spent more time in the zones near the white than the black walls during all three test sessions. For analysis, the results of all three test sessions conducted in this apparatus were entered into a three-way ANOVA. There was no overall difference between the hippocampal-BW and sham-BW groups, $F(1, 18) = 1.06$; and no difference between the three sessions, $F < 1$. Rats spent significantly more time in the zones near the white walls then the black walls, $F(1, 18) = 54.24$. There was no significant interaction between lesion and session, $F < 1$; nor between lesion and zone, $F < 1$; and no interaction between session and zone, $F < 1$. There was no three-way interaction, $F(2, 36) = 2.68$.

There are several intriguing features to these data. The purpose of providing feature information for the hippocampal-BW and sham-BW groups was to make location of the platform easier, but this was only partially successful. These groups took less time than those trained in the white rectangle to find the platform once the beacon was removed, but they made initial visits to the mid-points of the long walls no more often. During the first test trial, rats trained in the black and white rectangle spent more time than those in the white rectangle searching near the long walls. The overall impression from these data is that the black walls assisted rats' location of the platform to some extent. It is apparent that rats were able to learn about these walls by the preference for white over black walls shown during test trials in the black and white square.

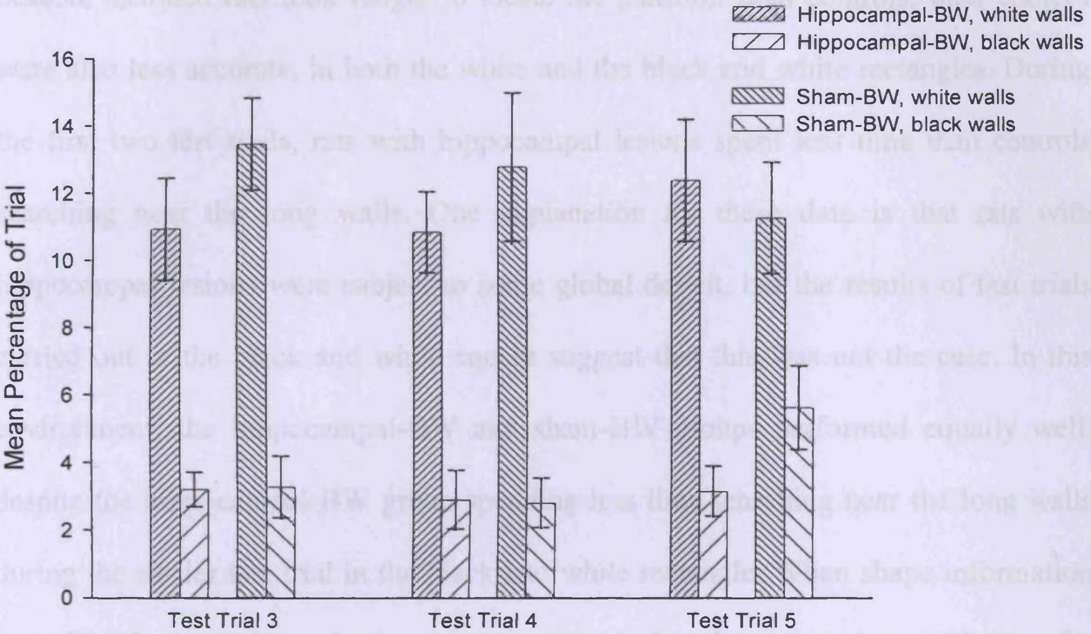

Figure 31. Results of the final three test trials, carried out in the black and white square. Scores represent the mean amount of these trials that rats in each group spent in 15 cm zones near the mid-points of the black and the white walls. Error bars represent ± 1 standard error.

The principle aim of this experiment was to compare the performance of rats with hippocampal lesions with controls. Generally speaking, lesioned rats performed more poorly than those who had received sham operations. Following removal of the beacon, lesioned rats took longer to locate the platform than controls; their choices were also less accurate, in both the white and the black and white rectangles. During the first two test trials, rats with hippocampal lesions spent less time than controls searching near the long walls. One explanation for these data is that rats with hippocampal lesions were subject to some global deficit, but the results of test trials carried out in the black and white square suggest that this was not the case. In this environment, the hippocampal-BW and sham-BW groups performed equally well, despite the hippocampal-BW group spending less time searching near the long walls during the earlier test trial in the black and white rectangle. When shape information as well as feature information was present, then, lesioned rats were impaired; once the shape information was removed and rats were able to use feature information only, hippocampally-lesioned rats were just as accurate as controls.

This pattern of results supports the idea that rats with hippocampal lesions were not able to use the information provided by the shape of the environment to find the platform as effectively as controls. Since the platform was located near to the mid-point of a long wall rather than near a corner, the only information that needed to be derived from the environmental shape to find the platform was the distinction of the long and the short walls. These results therefore tentatively support the idea that rats with hippocampal lesions are impaired at discriminating long from short walls.

One problem with this explanation is that the performance seen in the hippocampal-W group was far from poor. Their choices throughout training were comfortably above chance levels, and they spent much more time swimming near to the mid-points of the long than the short walls during test trials in the rectangular pool. Retrospectively, this may be explained by assuming that some other process took place when these animals were trained in the pool, which allowed rats with hippocampal lesions to spend more time near the long than the short walls without truly discriminating between them. Such explanations are decidedly *post-hoc*, but must be considered nonetheless. Suppose, for instance, that rats learned to find the platform based partially on its position in relation to the circular pool into which the rectangle was placed. The areas adjacent to the mid-points of the long walls are closer to the centre of the circular pool than the equivalent areas near the short walls; a strategy based on swimming in the middle of the circular pool would be capable of producing an apparent preference for the long walls over the short walls, without requiring the animals to learn anything about lengths. There are various visual cues which might allow animals to localise the middle of the pool, such as proximity to the curtain surrounding the pool, and the camera positioned in the ceiling above the centre.

It seems possible that I did not gain control over the cues governing rats' behaviour, and a different approach is needed if I am to draw any firm conclusions about the ability of rats with hippocampal lesions to discriminate lengths. To this end, a novel procedure was used in Experiment 5.

EXPERIMENT 5

Experiment 4 produced some tentative evidence that rats with hippocampal lesions are impaired in relation to controls at distinguishing between long and short walls. However, it is possible that I did not gain full control over the cues which rats used to orient; Experiment 5 attempted to remedy this problem by using a new procedure for testing the ability to discriminate lengths.

Rats were trained to find a platform in one corner of a square arena, with black panels fixed to the wall in each of a pair of opposite corners (Figure 32). One of these panels was twice the length of the other. The platform was located in one of the two corners which contained panels, and always stayed in the same place. I will refer to the corner containing the platform as the correct corner, and the opposite corner which contained a panel but no platform will be referred to as the incorrect corner. The rats used for this experiment were the same rats which made up the hippocampal-W and sham-W groups of Experiment 4; since they had already participated in one experiment, Experiment 5 lasted for only ten sessions. There were two groups (the hippocampal group and the sham group), with half the rats in each group trained to find the platform close to a long panel and half trained to find the platform near a short panel. On each trial throughout training, a record was taken of which of the two corners containing panels the rat visited first.

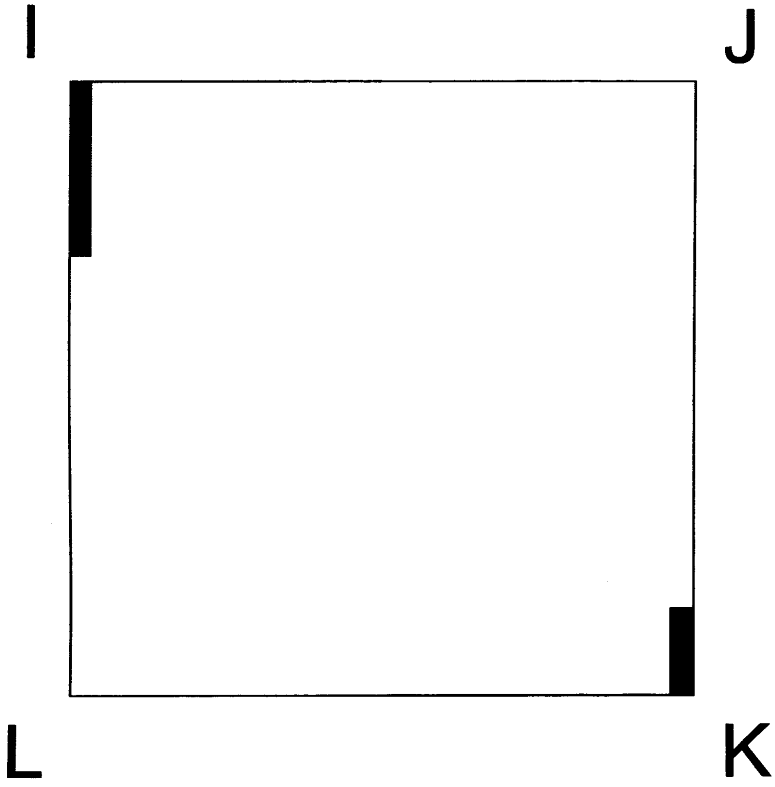

Figure 32. Schematic representation of the environment in which animals were trained during Experiment 5. Black Perspex panels were attached to the walls at two of the four corners of this square white-walled arena. In corner I, a panel of 40 cm length was attached to the left-hand wall (LI). At corner K, a panel of 20 cm length was attached to the left-hand wall (JK).

Method

Subjects and apparatus. The subjects were 23 male Hooded Lister rats, which had previously taken part in Experiment 4. There were 13 rats in the hippocampal group, and 10 rats in the sham group.

The square arena was constructed in a similar way as for previous experiments. It was composed of four white walls, each measuring 1.4 m in length. Panel inserts were made of black Perspex, attached to aluminium clips which held them onto the boards. One of the inserts was 40 cm in length and one was 20 cm, both were 40 cm high and 2 mm thick. They had one aluminium clip fixed onto the back; each clip was an inverted U-shape, with an aperture size of 25 mm, so that they fitted onto the top edges of the boards where the support bars were attached. The inserts could therefore be removably slotted onto the boards. One panel was attached to each of an opposite pair of corners of the square. In each corner, the panel was attached to the right-hand wall, immediately adjacent to the apex of the corner.

Procedure. Rats were transported to the room adjacent to the test room in groups of five, six, or seven. Each training session consisted of four trials, with rats allowed up to 60 s to locate the platform. Between each of the four trials, the square was rotated through 90 ° in a clockwise direction; for each trial in any given session, therefore, the square was in a different orientation. Rats were released from the mid-points of the four walls, facing the wall and with the four release points selected in a random order.

During all sessions of the experiment, the platform was located consistently one of the two corners containing panels; for seven rats in the hippocampal group and five in the sham group, it was located in the corner containing the long panels. The platform was located in the corner containing the short panel for the remaining rats. The centre of the platform was 25 cm from the corner of the square, along a notional line that bisected the corner. There were ten sessions in the experiment, with the beacon attached to the platform for the first five of these. For all trials within each of these sessions, the experimenter made a record of which of the two corners with inserts the rat visited first upon release. A choice was considered to have been made when a rat's head entered an arc-shaped zone centred on each corner and with a radius of 40 cm; a choice in the corner containing the platform, therefore, indicated that a rat had passed within 10 cm of the platform's edge.

Details which have been omitted were the same as for previous experiments.

Results

The rats used in Experiment 5 had previously taken part in Experiment 4; reconstructions of lesions are provided in Figure 26. Four rats from the hippocampal group were excluded due to insufficient cell loss in the hippocampus. The hippocampal group therefore contained nine rats.

Mean latencies for each stage of the experiment are shown in Figure 33. In general, rats found the platform much more quickly when the beacon was attached to the platform than when it was absent; rats with hippocampal lesions were also much slower than shams. For each rat, a mean latency was calculated for each of the two stages of the experiment, and these scores were entered into a two-way ANOVA. This analysis revealed an overall difference between the latencies to reach the platform before and after removal of the beacon, $F(1, 17) = 4.91$. The sham group took less

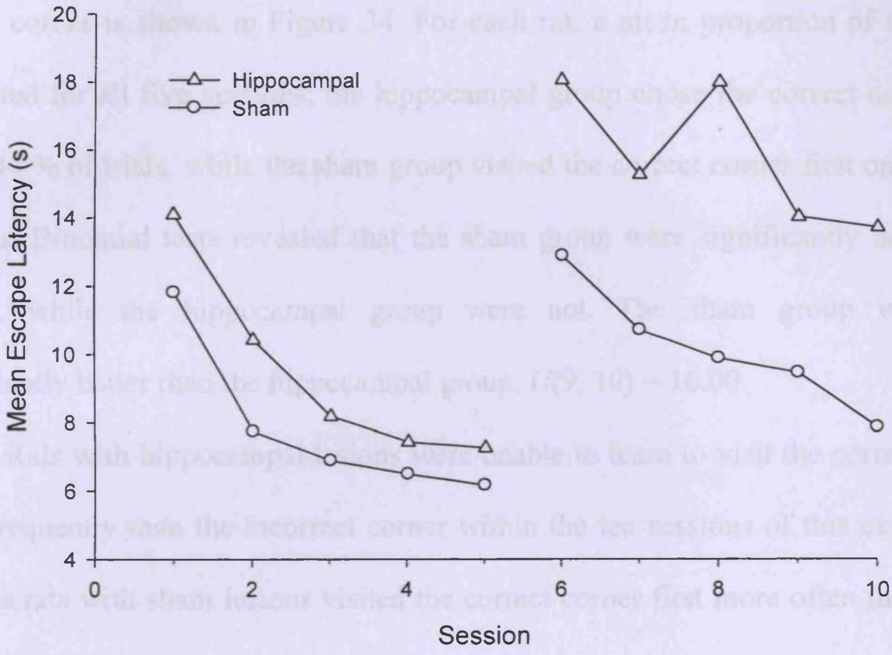

Figure 33. Mean escape latencies for the two groups of Experiment 5. All sessions were conducted in the square; the beacon was attached to the platform for sessions 1-5, and the beacon was absent for sessions 6-10.

time to find the platform than the hippocampal group, *F*(1, 17) = 8.88. There was no Lesion × Stage interaction, *F*(1, 17) = 1.88.

On each trial, a record was taken of which of the correct and incorrect corners was visited first. The mean proportion of trials on which rats initially visited the correct corner is shown in Figure 34. For each rat, a mean proportion of trials was calculated for all five sessions; the hippocampal group chose the correct corner first on 54.44 % of trials, while the sham group visited the correct corner first on 65.50 % of trials. Binomial tests revealed that the sham group were significantly better than chance, while the hippocampal group were not. The sham group were also significantly better than the hippocampal group, *U*(9, 10) = 16.00.

Rats with hippocampal lesions were unable to learn to visit the correct corner more frequently than the incorrect corner within the ten sessions of this experiment, whereas rats with sham lesions visited the correct corner first more often than would be expected by chance. This is line with the idea that the hippocampus is required for discriminating lengths. An additional possibility is that rats with hippocampal lesions simply learn such discriminations more slowly than shams, and that training here was not sufficiently extensive to allow the lesions rats to learn the task. Since the rats in Experiment 5 had previously taken part in Experiment 4, it was not possible to continue training beyond ten sessions; a future experiment should remedy this. Nevertheless, the results of Experiment 5 show that rats with hippocampal lesions are impaired on a task which requires the discrimination of lengths.

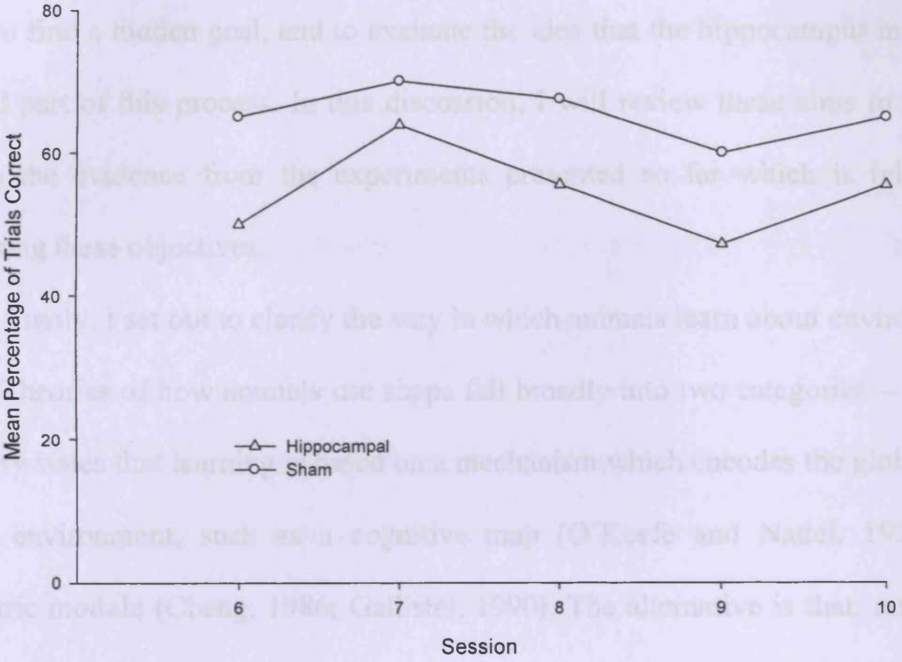

Figure 34. The mean percentage of trials on which rats in the two groups of Experiment 5 entered the correct corner before the incorrect corner after removal of the beacon.

DISCUSSION

I have previously outlined two main aims of this thesis: to provide further insight into the manner in which animals use information provided by environmental shape to find a hidden goal, and to evaluate the idea that the hippocampus may be an integral part of this process. In this discussion, I will review these aims in turn and discuss the evidence from the experiments presented so far which is relevant to addressing these objectives.

Firstly, I set out to clarify the way in which animals learn about environmental shape. Theories of how animals use shape fall broadly into two categories – one type of theory states that learning is based on a mechanism which encodes the global shape of the environment, such as a cognitive map (O'Keefe and Nadel, 1978) or a geometric module (Cheng, 1986; Gallistel, 1990). The alternative is that, rather than using global cues, animals use local cues to orient (Pearce et al., 2004; Tommasi & Polli, 2004). Experiments 1 and 2 were designed to provide some decisive evidence, and the overall impression gained from the results is in line with the proposed local account. When trained to find a hidden platform in one corner of a rectangular arena, rats quickly learned to do so; moreover, when placed into an environment with a different global shape but which preserved some local cues, rats demonstrated a pattern of behaviour which was consistent with the continued use of that local information (sham-W group, Experiment 1). A similar result was obtained for rats trained initially in a kite-shape arena before being transferred into a rectangle (sham-90 group, Experiment 2). I interpreted these results as being a forceful demonstration of rats' use of local cues. Once placed into an arena with a new global shape, animals would not have been expected to show a preference for any particular area of the pool if learning in the original arena had progressed according to global information, unless the global representation permitted the derivation of local information (in the case of cognitive maps, such a provision has been made by O'Keefe, 1991).

A new conception of purely global cues can, however, provide an account of these data. Since their publication (Pearce, Good, Jones, & McGregor, 2004), Cheng and Gallistel (2005) have given an explicit account of how transfer of learning between environments may occur, even when the original strategy for finding the platform was based on a global representation. This conception does not require the consideration of rats' use of local cues. They suggested that a global representation need not capture every facet of the shape of the environment; rather, it may consist of an abstracted set of parameters which capture various properties of the shape. Cheng and Gallistel focussed on a parameter known as the principal axis, an axis which passes through the centroid of a shape. This is the axis about which rotating the shape will produce minimal angular acceleration. The axis is derived from the overall shape of the environment, but does not capture every feature of it. Learning in one environment may transfer to another, they argue, by alignment of the principal axis of the old environment (stored in memory) with the principal axis in the new shape. This does not require a total match, merely that a principal axis may be identified for each shape.

Cheng and Gallistel (2005) applied this idea to the results observed in the sham-W group of Experiment 1. In the rectangular arena, the principal axis runs parallel to the two long walls, equidistant from each (Figure 35, top panel). Suppose that the platform was located in corner A or corner C; these corners are located to the right-hand side of each end of the principal axis. It is possible that rats learned to find the correct corners by swimming along the principal and veering to the right. Now

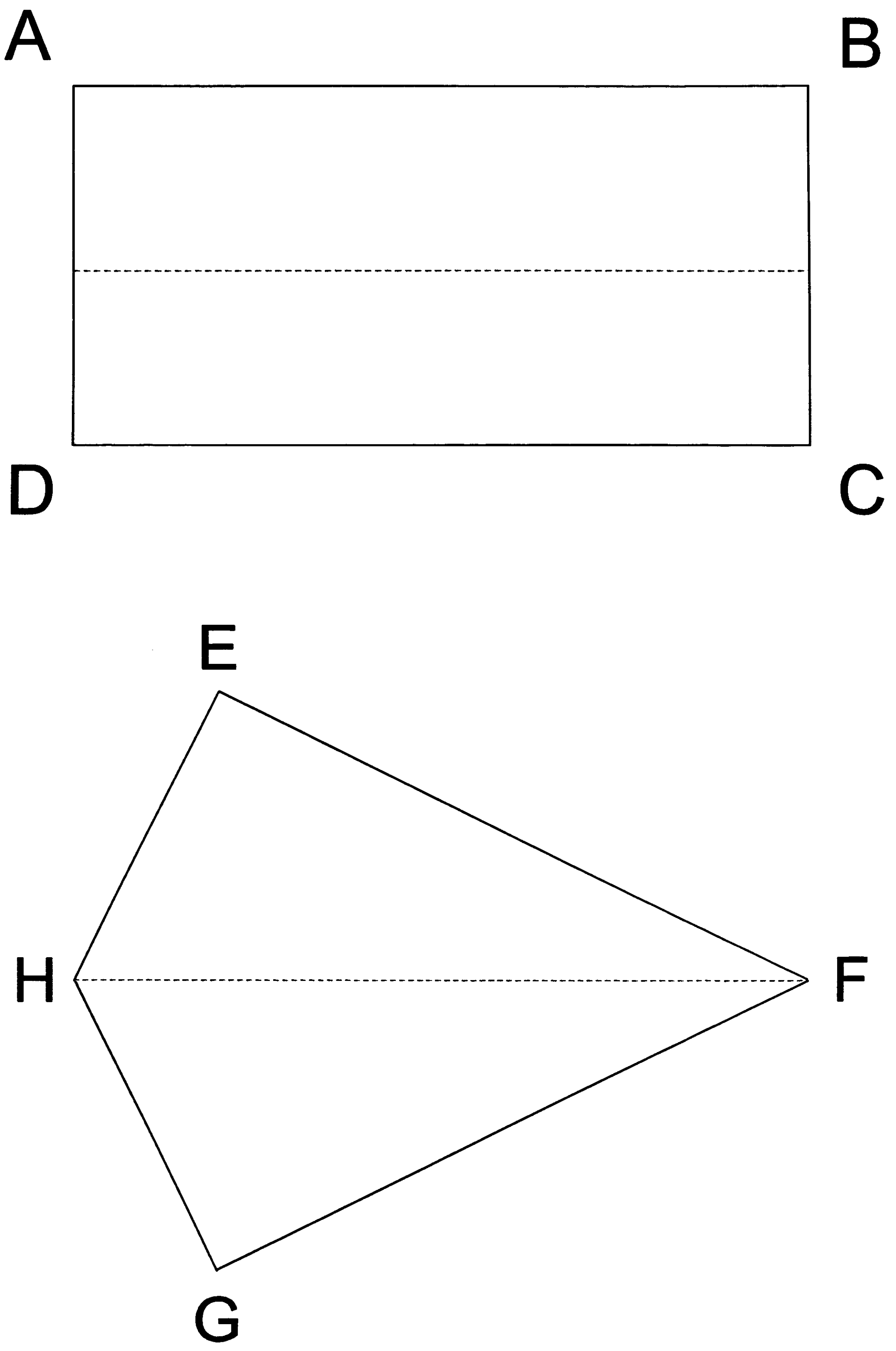

Figure 35. Rectangular and kite-shaped environments, with principal axes superimposed (broken lines).

consider the kite-shaped arena; the principal axis here runs from corner F to corner H (Figure 35, lower panel). If rats attempted to use their already-acquired strategy of swimming to the right of the ends of the principal axis in the kite, they would find themselves at either corner E or corner F. This is the same prediction as made by an account based on use of the long walls as local cues. Cheng and Gallistel suggest, then, that this kind of global cue account explains neatly the transfer of behaviour seen when animals trained in the rectangle are placed into the kite. Similar interpretations are possible for the results of Experiment 2, and Tommasi and Polli (2004).

Although these results can be explained by appealing to global parameters based on shape rather than the shape of the environment itself, they can be accounted for just as easily by assuming that rats used local cues. Furthermore, the complexity involved in calculating parameters such as principal axes is prohibitive. In the rectangle, it seems fairly intuitive that the principal axis runs through the middle of the rectangle, along its longest dimension. In some other shapes, however, it is not obvious where the principal axis should lie (Tommasi, 2005). Ease of computation must surely be a prerequisite for any representation upon which animals rely for a process as vital as navigation. Tommasi also draws attention to the need for an environment to be observed in its entirety before such parameters can be computed. As a result, an animal using this type of representation would need to survey the boundary of the entire environment before it was able to orient itself. This seems unlikely to be the case, although this idea is readily testable.

It is also difficult to see how a process of generalising from one environment to another based on global shape parameters would be of use to animals. Since multiple environments will have similar principal axes, what is learned in one environment will be applied to another, as is supposedly the case in Experiment 1. There seems to me to be little reason to assume that two environments with similar principal axes should share the same properties. Rather, this generalisation will often be inappropriate, as animals apply what is learned in one environment to another very different and unrelated environment. A more useful strategy is surely the association of hidden goals with local cues which commonly occur in close proximity. Since the same type of local cue can occur in a variety of different environments, there is good reason for animals to behave in a new environment in a manner which is consistent with local cues that they have encountered before. Nevertheless, I am unable to firmly conclude on the basis of the data I have presented so far that this process of axis matching is incorrect. Any transfer test for which this process and local cue accounts make the same prediction is unable to give much insight into which process is responsible for navigation in the original arena. What is needed for their distinction is some test for which the global and local accounts make differing predictions.

Such a test has recently been conducted by McGregor, Good, Jones, and Pearce (2005). Rats were trained to find a platform located in one corner of a pentagonal arena (Figure 36), constructed within a circular pool. One end of the pentagon resembled a rectangular arena, and was composed of a long wall (OP) with a short wall adjoining at either end. An additional wall joined onto each of the short walls, with these meeting at an apex at corner M of the pentagon. Rats were trained to find a platform hidden in corner O or corner P, before being placed into a new arena. The principal axis of the pentagon ran from corner M to the mid-point of wall OP. Rats may have learned to find the platform based on such a global parameter, or on a local cue such as the position of wall OP in relation to the platform. Rats were tested in a rectangular arena; the two strategies just described made differing predictions for

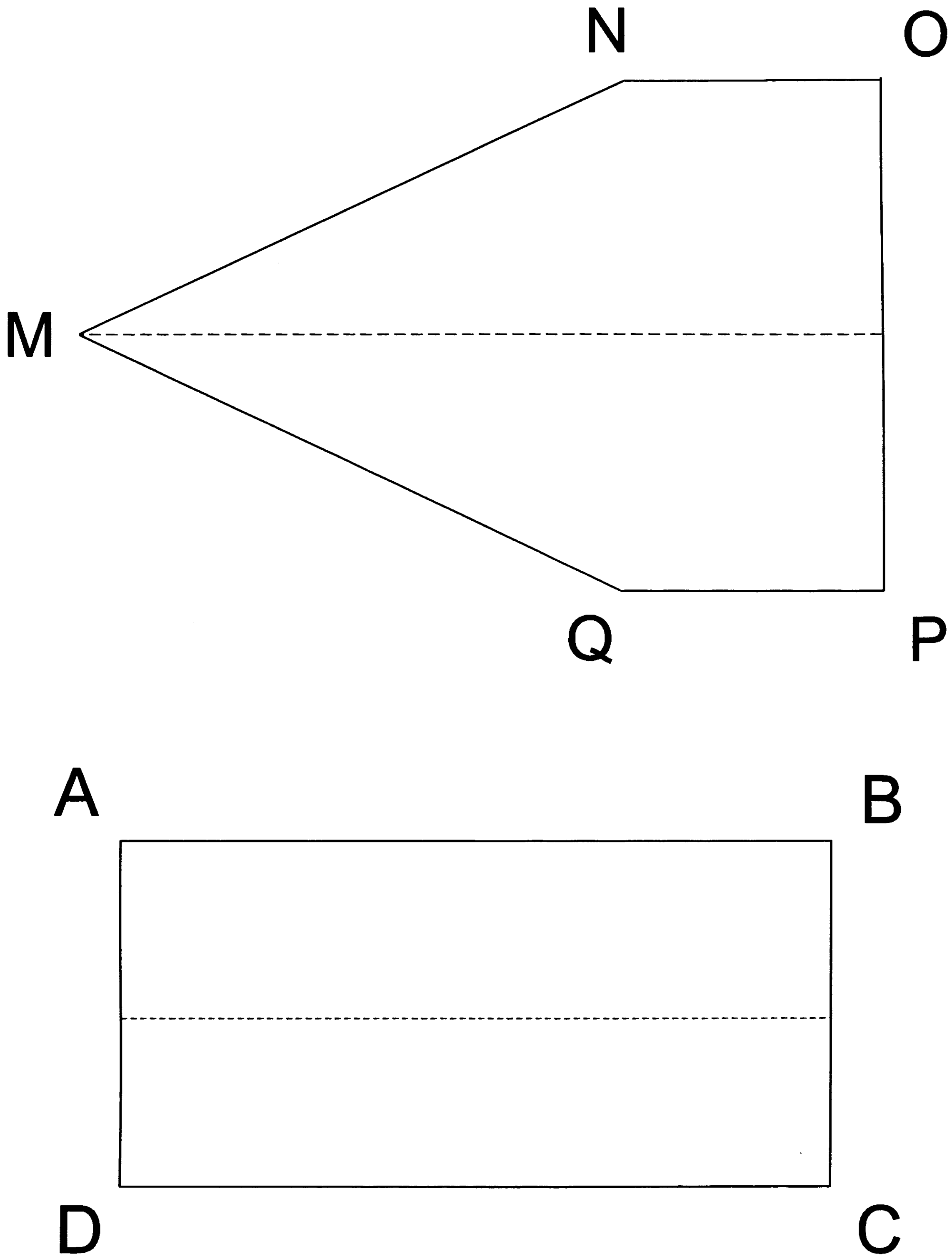

Figure 36. Schematic representations of the pentagonal environment used by McGregor et al. (2004, top panel) and a rectangular environment (lower panel), with principal axes superimposed.

rats' behaviour when placed into this new pool. If they generalised from the pentagon to the rectangle by aligning principal axes, then they would be expected to search at corners which were not consistent with the platform's former relationship with local cues. In fact, rats, spent most time searching in corners which had the same local properties as the corner in which the platform had been located in the pentagon. This behaviour was inconsistent with the idea that rats matched the two environments on the basis on their principal axes. It is difficult to see how any explanation based on global shape parameters can account for this result.

An additional test trial was conducted in a shape that was similar to the original pentagon, except that wall OP was removed. The new shape (bounded between corners O and P by an arc of the circular pool in which arenas were constructed) had a similar principal axis to the original pentagon, but was missing a local feature which had been located near the goal. During this test trial, the amount of time searching near corners O and P was measured. If rats were able to use the strategy they had acquired in the pentagon, they should have spent more time searching near the corner where the platform had been located than the corner where it had not. This was not the case – rats demonstrated no preference for either one of these two areas over the other. Presumably, they were unable to orient effectively because the wall which was removed had acted as a crucial local cue.

It seems unlikely, then, that navigation in the pentagon was governed by the use of global cues. Rather, rats used local information to find the platform. These results are another demonstration that rats are able to use local cues to find a hidden goal. It is possible that animals are able to use both local and global cues to orient by information provided by shape, although there is no reason to entertain this idea. Local cue explanations account for all the data presented in this thesis and elsewhere.

While there is clear evidence that animals are capable of using local cues in an environment with a distinctive shape, there is no evidence available yet which demonstrates the use of global cues. For the idea that animals are sensitive to this type of information to be entertained, this evidence is surely long overdue.

The role of the hippocampus in the use of information provided by shape is closely related to the discussion above. In Experiment 1, the hippocampal-W group were impaired in relation to the sham-W group, indicating the importance of the hippocampus for accurate use of the information provided by the walls of a featureless rectangle. This result was replicated in Experiment 3. As I summarised earlier, although the hippocampus has been cited as the location of a global representation (O'Keefe and Nadel, 1978), there is little evidence capable of supporting this idea. I stated that in order to substantiate claims of a hippocampal-dependent global representation, there was a need to observe a deficit following hippocampal lesions on a task which can be shown to be reliant upon the use of global cues. However, as discussed above, the comparison of lesioned and control groups in featureless arenas here does not meet these criteria. Controls groups located the platform in these arenas by using local cues, and I am compelled to conclude that the hippocampus is important for navigation based on local cues.

Additional results from the first three experiments here show, however, that not all local processes are abolished following hippocampal damage. Rats with hippocampal lesions were able to use black walls to orient, either when these walls were close to the platform (Experiment 1) or when they were further away (Experiment 3). They were also able to discriminate between corners in a featureless arena under at least some circumstances (Experiment 2), even if they did so less accurately than controls. Such results suggest a specificity in the deficit observed following hippocampal lesions, such that discrimination of corners in a featureless rectangle is affected but some other processes are not.

The possible explanation tested towards the end of this chapter was that rats with hippocampal lesions are unable to accurately tell the difference between the long and the short walls of the rectangle. This would explain their inability to use a simple strategy based on a single wall. The results of Experiments 4 and 5 provided tentative support for this idea; although rats with hippocampal lesions searched more frequently near the long than the short walls in Experiment 4, it is possible that this was a result of an additional process, unrelated to the discrimination of lengths. However, this explanation is somewhat speculative, and the idea that the hippocampal-W group of Experiment 4 performed well because they were able to tell the difference between long and short walls cannot conclusively be discounted. If my reasoning is incorrect, and rats with hippocampal lesions can discriminate between these different lengths of walls, then an alternative explanation of the deficit observed in Experiments 1 and 3 must be sought.

It is possible, for instance, that the hippocampus has some non-spatial role in stimulus learning which is important for navigation in a featureless rectangle but not in one which contains additional features. Rudy and Sutherland (1995) have suggested that the hippocampus may be involved in facilitating learning about stimulus configurations by raising the salience of relevant cues. In the tasks I have described, this can be interpreted as facilitating learning about the walls of the arena. In the black and white arenas used in Experiments 1 and 3, the black walls may be sufficiently salient that animals are able to learn to find the platform without any hippocampal involvement; the relative salience of the long walls when compared with the other sides of a featureless rectangle, however, may be lower. The hippocampus might be needed to 'boost' the salience of stimuli in this arena, which would explain why rats with hippocampal lesions have difficulty learning this task.

In order to draw firmer conclusions about the exact role the hippocampus plays in finding the platform in a rectangular arena, some further testing is needed. Principally, it would be interesting to explore more fully the idea that rats with hippocampal lesions are not able to accurately discriminate between the two different lengths of walls. One line of enquiry might be that taken in Experiment 5, although testing rats' accuracy at discriminating between two different lengths of panel is not directly equivalent to assessing their ability to discriminate between walls that make up the large-scale shape of their environment. In the watermaze, it is not clear how this could be achieved without encountering the sort of confound present in Experiment 4.

In summary, the results obtained by comparing the performance of hippocampally-lesioned animals with controls do not make the role of the hippocampus explicit; but they are a forceful demonstration that the hippocampus at least has a role in the use of local geometric information.

CHAPTER THREE

EXPERIMENT 6

In the experiments presented so far, I have demonstrated that rats with hippocampal lesions are impaired at orienting according to information provided by the shape of an arena. In all of these experiments, lesions were administered prior to the onset of training; as a consequence, rats with hippocampal lesions were impaired throughout acquisition. One limitation of this method of enquiry is that because lesioned animals were not able to learn based on the information provided by shape, these experiments do not tell us anything about the role of the hippocampus in using shape-based strategies which have already been learned. Experiment 6 attempted to address this problem.

There are two methods by which the role of the hippocampus in retrieval and use of spatial memories can be assessed. The first was employed by Bolhuis, Stewart, and Forrest (1994), who administered lesions after acquisition of a spatial task. Rats were trained to find a platform in a circular watermaze, before being subjected to either a hippocampal lesion or a sham surgery. During acquisition, all animals learned to find the platform effectively. Following training, surgeries were carried out. In a subsequent retention test, hippocampally-lesioned animals spent no more time searching in the area of the pool where the platform had been than would be expected by chance. Sham operated animals, meanwhile, displayed a strong preference for the correct area of the pool. Although both groups had been able to learn to find the platform during the acquisition phase, those animals which had subsequently received hippocampal lesions were impaired at test.

Hippocampal lesions, then, produced a marked impairment in the retrieval of a spatial strategy that was learned pre-operatively. A second method of assessing the role of the hippocampus in retrieving these strategies is to temporarily impair hippocampal function after acquisition. Moser And Moser (1998) have shown a decrease in performance on a spatial watermaze task requiring the use of extra-maze cues after temporary deactivation of a portion of the hippocampus between acquisition and test phases. Rats were trained on a task similar to that used by Bolhuis et al. (1994), and subsequently tested by being placed into the pool in the absence of a platform and allowed to swim freely. Immediately prior to this test trial, half the rats received an intrahippocampal infusion of saline, while the other half received an infusion of the $GABA_A$ agonist muscimol. This compound was expected to disrupt synaptic transmission, by disabling the brain region into which it was infused; rats receiving this compound were expected to be subject to hippocampal deactivation, while those receiving saline had normal hippocampal function. Rats given saline subsequently spent a higher proportion of the test trial swimming in the area which had previously contained the platform than any other, while those rats which had been given muscimol showed no such preference. Presumably, deactivation of the hippocampus rendered rats unable to use an already-acquired strategy for localisation of the platform. This reinforces the notion that the hippocampus is required not only for new spatial learning, but for the use of existing spatial memories.

This finding was elaborated by Riedel et al. (1999). Rats were trained to find a hidden platform in a watermaze, and subsequently tested in the absence of the platform in the way previously described. Throughout the experiment, rats were given intrahippocampal infusions of one of two solutions; one was a vehicle solution, which was not expected to affect hippocampal function, while the other was a solution containing a drug which blocks synaptic receptors. This latter infusion was expected to disrupt hippocampal function. Each rat received the same infusion prior to each training session; those rats which received the drug took consistently longer to find the platform than those which received the vehicle infusion. Prior to the test session, half the rats in each group received an infusion containing the drug, and the other half received vehicle. Those rats receiving the drug throughout training performed at chance levels on this test, irrespective of whether they also received the drug at test; interestingly, rats which had received vehicle infusions throughout training performed above chance only if they were also given vehicle prior to test. Those rats trained with vehicle but tested following a drug infusion performed at chance. This pattern of results suggests that the hippocampus is required for both the acquisition and the retrieval of the strategies necessary for successful performance of this spatial task.

In this thesis, I have already shown that hippocampal lesions impair the ability of rats to navigate based on information provided by the shape of the environment; in Experiment 6, I assessed the extent to which the hippocampus is required for the retrieval and use of such strategies. This was done by training rats to find a hidden platform in one corner of a rectangular watermaze (Figure 37, top panel), and deactivating the hippocampus between acquisition and test.

Cannulas were implanted into the dorsal hippocampus prior to the onset of training, and infusions were given via these cannulas prior to each test trial. On test trials, rats were released into the pool in the absence of a platform, and allowed to swim freely for 60 s. If animals are able to discriminate between corners, they should spend more time near the correct pair or corners than the incorrect pair. Three test trials were carried out: one with no infusion, one following an infusion of CNS perfusion fluid, and one following an infusion of muscimol dissolved in CNS

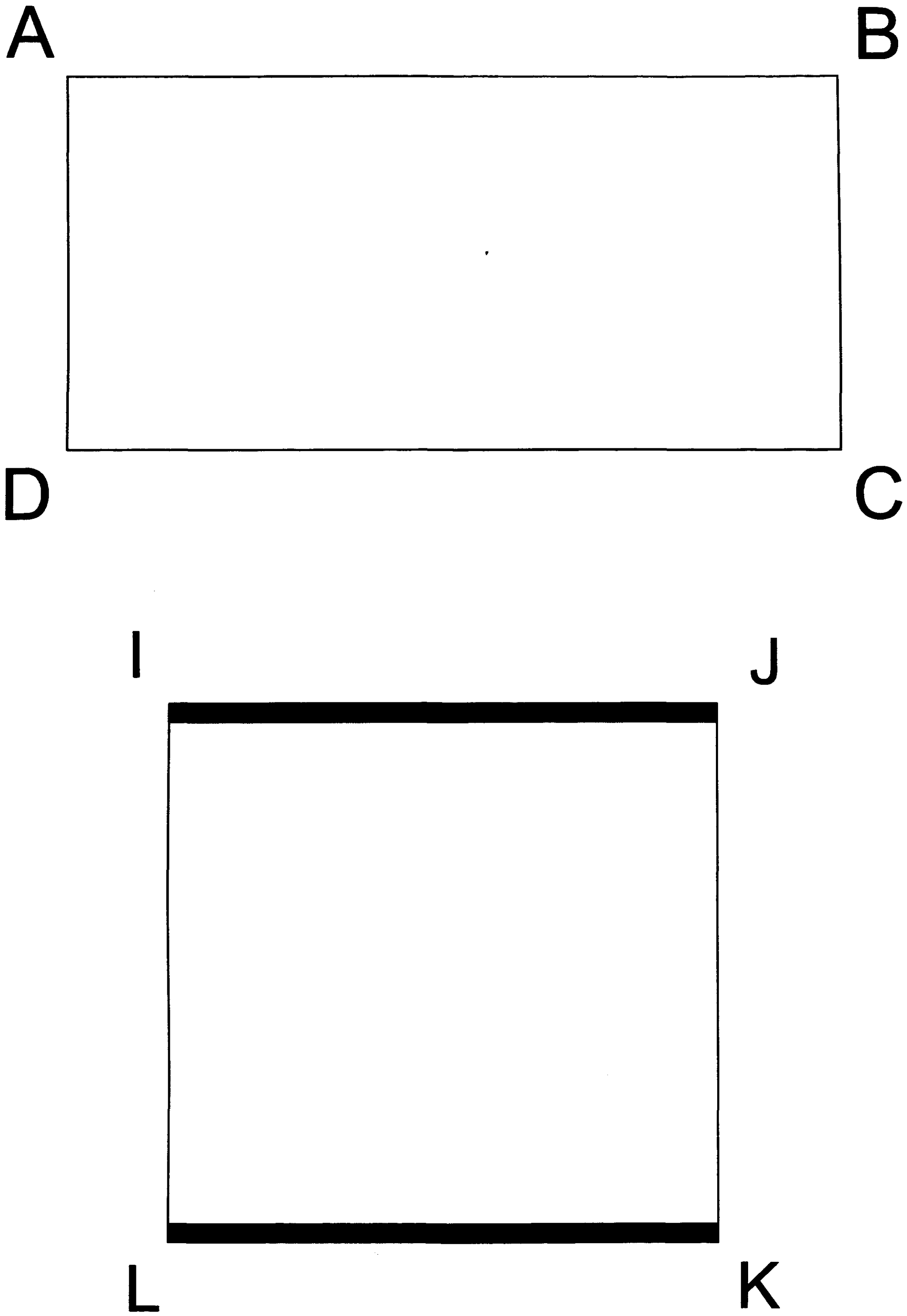

Figure 37. The two test environments in which rats were trained during Experiment 6. In two separate stages, rats were trained to find a platform in a white rectangle (top panel) and a square environment with matching opposite pairs of black and white walls (lower panel).

perfusion fluid. The order in which these test trials were carried out was varied. While infusions of perfusion fluid were not expected to disrupt hippocampal function, infusions containing muscimol were expected to produce deactivation of the dorsal hippocampus; poorer performance in the test trial immediately after muscimol infusion than the remaining two test trials would therefore indicate a role for the hippocampus in the retrieval of a strategy based on information provided by shape. The effect of muscimol was not expected to exceed 24 hours, and retraining sessions were given between tests.

One problem with previous experiments using hippocampal deactivation (Moser & Moser, 1998; Riedel et al., 1999) is that they have not assessed the effect of infusions upon tasks which are hippocampal-independent. Without a demonstration of good performance after drug infusions on a comparable task which does not require the hippocampus, it is possible that any deficit on a spatial task is due to a general disabling effect, rather than any specific role of the hippocampus in spatial behaviour. To counter this possibility, in Experiment 6 rats were trained and tested in an additional arena. This was a feature-based watermaze task, in which animals were required to locate a platform in one corner of a square arena with two black walls and two white walls (Figure 37, lower panel). Each pair of opposite walls was the same colour. McGregor et al. (2004) have shown that under these conditions, rats with hippocampal lesions choose the correct corners over the incorrect corners as frequently as controls; orientation according to the walls of this environment was not expected to require the hippocampus. I expected, therefore, to see no effect of muscimol infusions on performance levels in this square arena.

Method

Subjects and apparatus. The subjects were 12 male rats from the same stock and housed in the same manner as for previous experiments. During the experiment, one rat became ill and was withdrawn from the experiment.

Four Perspex boards were used to create each of the rectangular and the square pools. The rectangle was constructed in the same way as for previous experiments; the square was similar, except that each board was 1.4 m in length. Two walls of the square were coloured white, and two were coloured black. Walls of matching colour were positioned opposite each other, so that any two adjacent walls were in contrast with one another. The bars attached to the black walls overlapped and rested on the bars attached to the white walls. Other details of the apparatus were the same as for previous experiments.

Surgical procedure. One week before the onset of behavioural training, the rats were implanted with stainless steel guide cannulas aimed at the dorsal hippocampus. The rats were deeply anaesthetized using a mixture of isoflurane and oxygen, and mounted in a Kopf stereotaxic frame (Kopf Instruments, Tujunga, CA). Anaesthetic was then reduced to a maintenance concentration, and an incision was made along the midline of the scalp. The pericranium was retracted, and five small burr holes (1 mm in diameter) were drilled into the skull. Two of these were for bilateral placement of a stainless steel guide cannula (26 gauge; 7 mm in length; Plastics One, Roanoke, VA) into the dorsal hippocampus (3.0 mm posterior to bregma, 1.5 mm lateral to bregma, and 2.5 mm ventral to dura). Small jeweller's screws were placed into the remaining three. Dental acrylic was used to affix the cannula to the skull and to seal the scalp incision. After surgery, stainless steel dummy cannulas (33 gauge; 8.5 mm in length; Plastics One) were inserted into the guide cannulas, and dust caps (Plastics One) were screwed onto the end.

Infusion procedure. Rats were transported to the infusion room in groups of six, in a carry box. Each rat was in turn taken out of the box, and wrapped in a small towel to restrict movement. The dust caps and dummy cannulas were removed, and replaced by 33 gauge internal injection cannulas (Plastics One), which extended 1.5 mm beyond the end of the guide cannulas. The injection cannulas were attached to polyethylene tubing, which was in turn connected to 1 µl Hamilton syringes mounted in an infusion pump (Harvard Apparatus, Edenbridge, UK). Rats were administered an infusion of either CNS perfusion fluid (CMA Microdialysis, N. Chelmsford, MA) or muscimol (Sigma Chemical, St. Louis, MO; 1 µg/µl dissolved in perfusion fluid). A total volume of 0.5 µl was infused into each hemisphere over a 60 s period; for those infusions containing muscimol, this yielded an infusion of 0.5 µg of muscimol into each hemisphere. During infusion, the experimenter distracted rats with finger pokes and verbal clicks, as cannulas were easily dislodged by movement of the animals. After infusion, cannulas were allowed to remain in place for 90 s. Injection cannulas were then removed, and dummy cannulas and dust caps replaced. Rats were then returned to their home cages. Approximately one hour after the infusion, the rats were transported to the watermaze test room for behavioural testing.

Experimental procedure. Rats were taken to the test room in groups of six. All groups received three sessions of pretraining in a circular watermaze, with animals required to locate the platform, which had the beacon attached to it. During sessions

4-21, rats were trained in the rectangular pool with the centre of the hidden platform located 25 cm from one corner. For half the rats the platform was located in either corner A or corner C, and for the other half it was located in either corner B or corner D (see Figure 37). During sessions 4-11, the beacon was attached to the platform.

Session 22 consisted of one test trial only. Rats were allowed to swim freely in the absence of a platform for 60 s before removal from the pool. After this test session, more training sessions were administered in order to restore any learning that had been extinguished during the test. Rats were therefore trained in the manner described before during sessions 23-26. Session 27 consisted of one test trial. Rats were then trained in the rectangular pool during sessions 28-31, before being tested or the third time during session 32.

Each of the three test sessions consisted of only one trial. Prior to the first test session, no infusions were given to any animal. For the second and third test sessions, animals were given either an infusion containing muscimol or a control infusion, according to the procedure outlined above. Half the animals received the control infusion prior to the second test session and the muscimol infusion prior to the third; infusions were administered to remaining animals in the reverse of this order.

After all sessions in the rectangle had been completed, training commenced in the black and white square. Rats were trained during sessions 33-40 in the square pool, with the beacon attached to the platform for the first 3 of these. The procedure was similar to that outlined for the rectangular pool above, with half the rats trained to find the platform in corners A and C, and the remainder trained to find the platform in corners B and D (see Figure 37). Animals were again given three test sessions, the first of which was conducted as session 41. Rats were given training trials on sessions 42 and 43, before the second test was conducted on session 44. Sessions 45 and 46 then consisted of further training trials, before rats were given a third and final test trial in the square on session 47. Prior to the second of these three test sessions, no infusions were given. Either muscimol or a control infusion was given to each rat prior to the first and third test sessions, with half the rats receiving the muscimol infusion first and the other half receiving the control infusion first.

Procedural details that have been omitted were the same as for previous experiments.

Results

Figure 38 shows sites of cannula placement for nine animals on a series of coronal sections taken at distances in mm posterior to bregma (top to bottom: -2.30, -2.56, -2.80, -3.14 mm). For these animals, all placements were within the dorsal hippocampus. Placements could not be found for the remaining two rats; results obtained with these rats did not differ from others, so they were included in the following analyses.

Rectangular arena. Figure 39 shows the group mean escape latencies for each training session conducted in the circular pool and the rectangular arena, both with and without the beacon attached to the platform. Sessions 1-3 were conducted in the circular pool with the beacon attached to the platform, and the beacon was still present during sessions 4-11, which were carried out in the rectangular pool. Although latencies to locate the platform became much longer following removal of the beacon, they decreased rapidly during the subsequent sessions. After removal of the beacon, performance was also assessed by keeping a record of which corner rats entered first

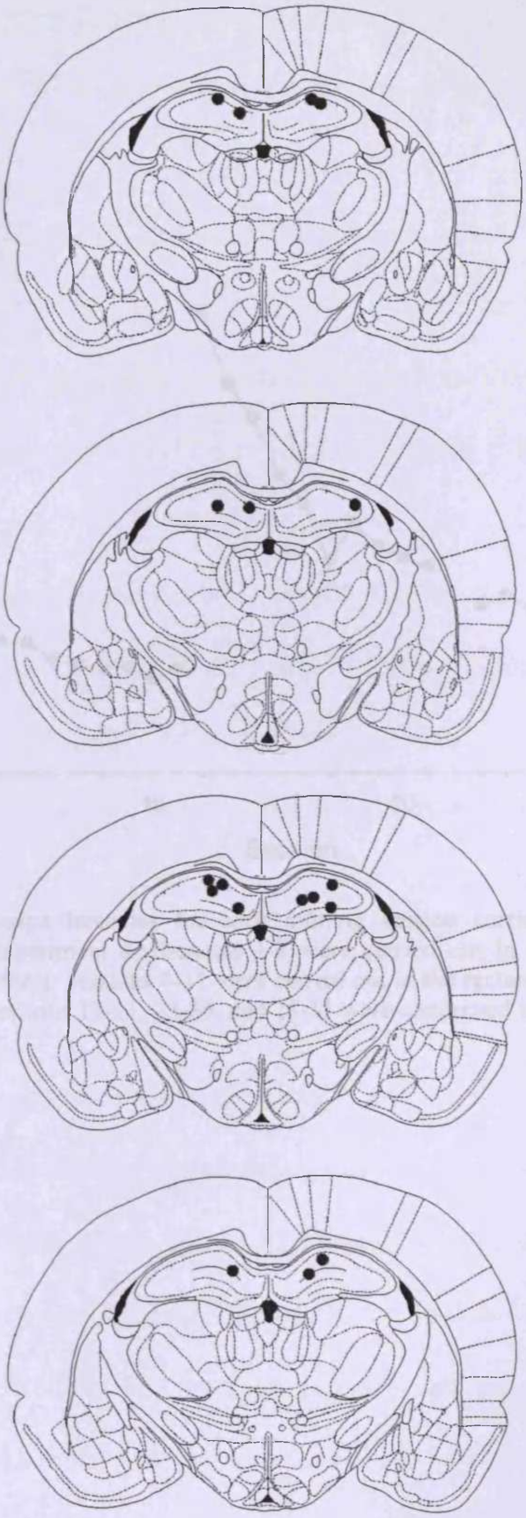

Figure 38. Cannula placement sites for Experiment 6. Sites are indicated by black circles.

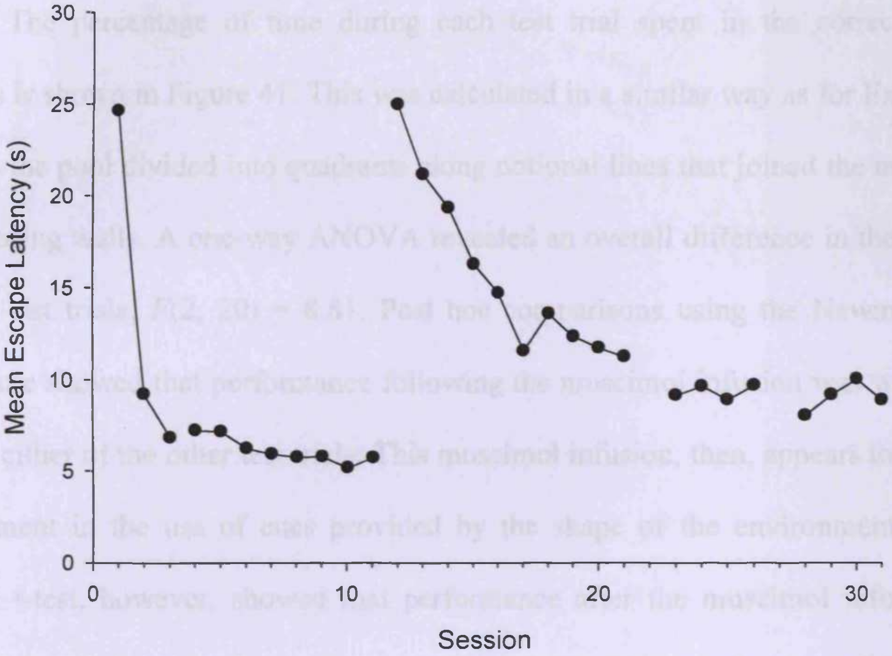

Figure 39. Mean escape latencies for each training session carried out in the circular or rectangular pool during Experiment 6. Sessions 1-3 were carried out in the circular pool with the beacon attached to the platform; sessions 4-11 were carried out in the rectangular pool with the beacon attached to the platform; sessions 12-21, 23-26, and 28-31 were conducted in the rectangular pool with the beacon removed.

upon release – one of the two correct corners, or one of the two incorrect corners. Rats showed a high level of performance on this measure throughout training, with rats visiting correct corners first on more than 84 % of trials in every session (see Figure 40).

The percentage of time during each test trial spent in the correct pair of corners is shown in Figure 41. This was calculated in a similar way as for Experiment 1, with the pool divided into quadrants along notional lines that joined the mid-points of opposing walls. A one-way ANOVA revealed an overall difference in these scores among test trials, $F(2, 20) = 8.81$. Post hoc comparisons using the Newman-Keuls procedure showed that performance following the muscimol infusion was worse than during either of the other test trials. This muscimol infusion, then, appears to cause an impairment in the use of cues provided by the shape of the environment. A one-sample t-test, however, showed that performance after the muscimol infusion was better than that expected by chance, $t(10) = 3.02$. This result is possibly due to incomplete deactivation of the hippocampus by muscimol infusions.

Since a deficit was observed between performance after the control infusion and performance following infusion of muscimol, we can rule out any suggestion that the process of infusion in itself is responsible for this impairment. Rather, the effect of the muscimol in deactivating the dorsal hippocampus caused animals difficulty in using information provided by the shape of the arena. Since infusions were administered between training and test, we can say that the hippocampus must be involved at the stage of retrieving and using shape-based strategies.

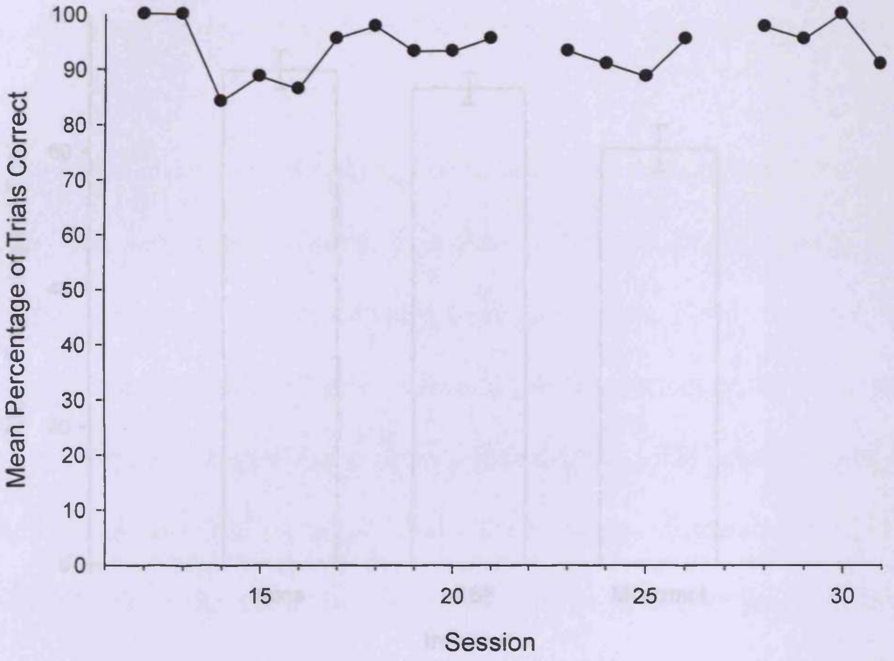

Figure 40. The mean proportion of trials on which rats entered a correct corner before an incorrect corner during training trials carried out in the rectangular pool during Experiment 6.

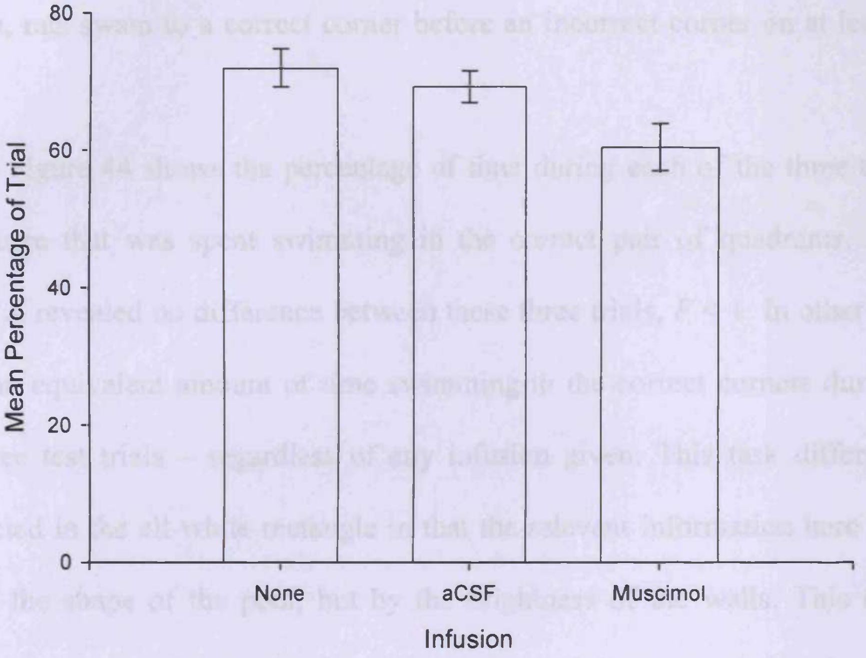

Figure 41. The mean percentage of each test trial carried out in the rectangle that was spent swimming in the quadrants near correct corners. The left-hand column represents the test trial conducted without any intrahippocampal infusion, the centre column represents the test trial which was preceded by an infusion of CNS perfusion fluid, and the right-hand column represents the trial which followed infusions containing muscimol.

Square arena. Figure 42 shows mean escape latencies for each training session in the black and white square pool. Rats appeared to rapidly learn to find the platform quickly in this arena. As shown in Figure 43, animals also visited correct corners first far more often than incorrect corners throughout training – during each session, rats swam to a correct corner before an incorrect corner on at least 93 % of trials.

Figure 44 shows the percentage of time during each of the three test trials in the square that was spent swimming in the correct pair of quadrants. A one-way ANOVA revealed no difference between these three trials, $F < 1$. In other words, rats spent an equivalent amount of time swimming in the correct corners during each of the three test trials – regardless of any infusion given. This task differs from that conducted in the all-white rectangle in that the relevant information here is provided not by the shape of the pool, but by the brightness of the walls. This dissociation between retrieval of strategies based on shape and features mirrors the findings of McGregor et al. (2004), who showed that the hippocampus was required for acquisition of a corner discrimination in a white rectangle, but not in a black and white square.

In the present experiment, rats were trained and tested in the white rectangle before the black and white square. Consequently, there is a possible order confound in that the effects of muscimol may have been effective only at first administration, reducing the likelihood of an impairment after the drug in the black and white square. Ideally, rats would have been given a final, additional set of test trials in the white rectangle with muscimol and control infusions in order to establish the permanence of the drug effect; this was not possible, as repeated infusions may introduce a greater likelihood of permanent tissue damage. However, a replication of these findings with

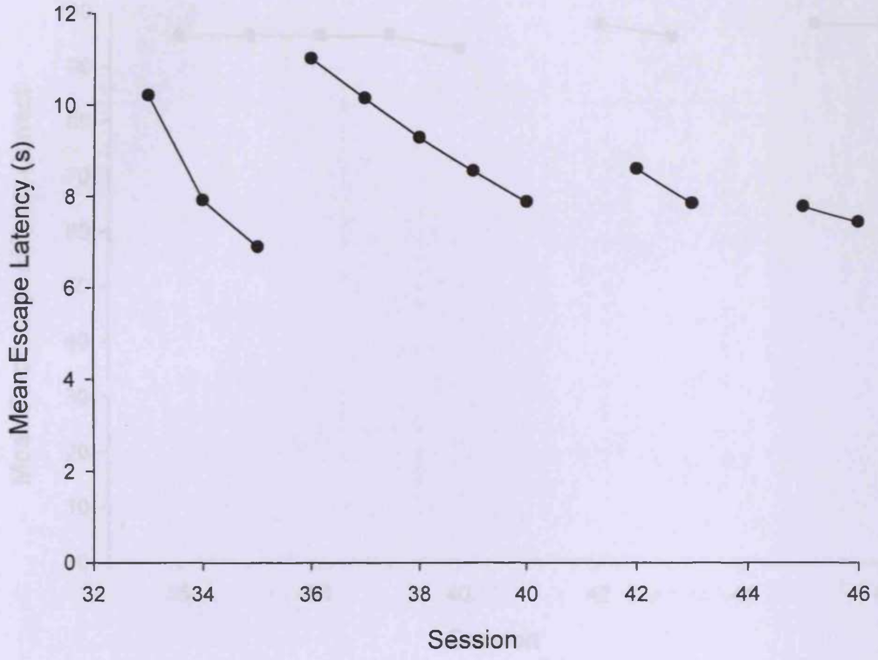

Figure 42. Mean escape latencies for each training session carried out in black and white square pool during Experiment 6. Sessions 33-35 were carried out with the beacon attached to the platform; sessions 36-40, 42-43, and 45-46 were carried out in the square pool with no beacon present.

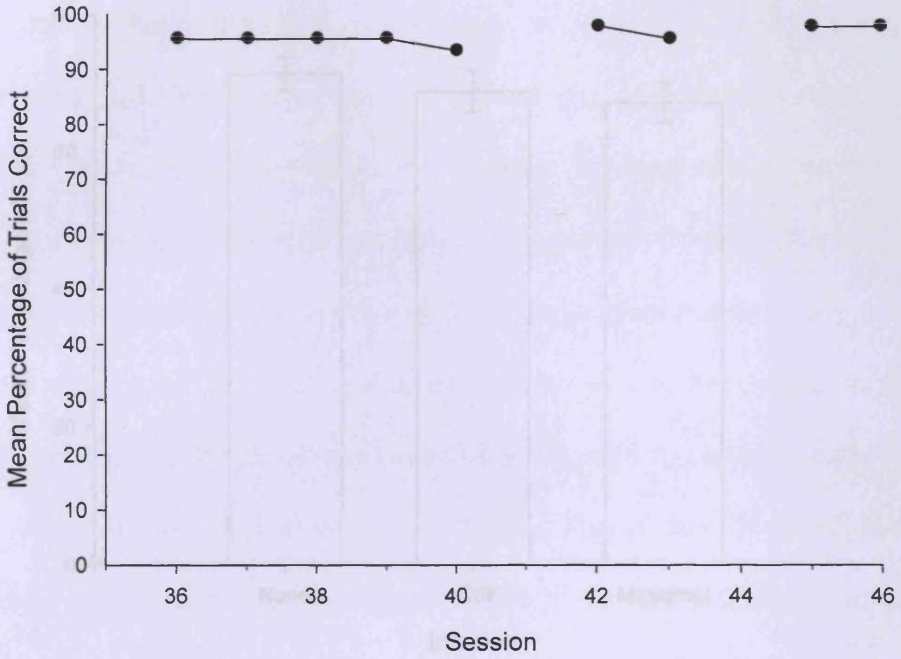

Figure 43. The mean proportion of trials on which rats entered a correct corner before an incorrect corner during training trials carried out in the square pool during Experiment 6.

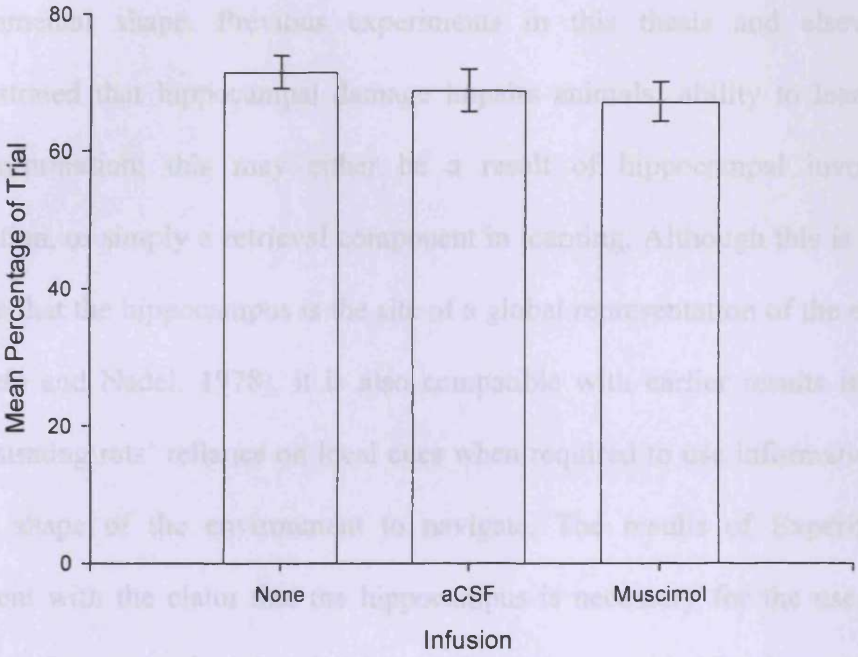

Figure 44. The mean percentage of each test trial carried out in the square that was spent swimming in the quadrants near correct corners. The left-hand column represents the test trial conducted without any intrahippocampal infusion, the centre column represents the test trial which was preceded by an infusion of CNS perfusion fluid, and the right-hand column represents the trial which followed infusions containing muscimol.

a reversal in the order in which the environments were used would be informative on this issue.

The results from Experiment 6 support the idea that the hippocampus is required for the retrieval of navigational strategies based on information provided by environmental shape. Previous experiments in this thesis and elsewhere have demonstrated that hippocampal damage impairs animals' ability to learn based on such information; this may either be a result of hippocampal involvement in acquisition, or simply a retrieval component in learning. Although this is in line with the idea that the hippocampus is the site of a global representation of the environment (O'Keefe and Nadel, 1978), it is also compatible with earlier results in this thesis demonstrating rats' reliance on local cues when required to use information provided by the shape of the environment to navigate. The results of Experiment 6 are consistent with the claim that the hippocampus is necessary for the use, as well as learning, of a strategy based on local cue information provided by shape.

What is less certain is how exactly the hippocampus is involved in both the acquisition and the subsequent use of a navigational strategy based on local information. One possibility is that the hippocampus is a mnemonic store (e.g. O'Keefe & Nadel, 1978), the loss of which renders animals unable to either form or recall memories which would otherwise enable efficient solution of the task. Another idea is that the hippocampus is involved in some perceptual process, which allows the animals to choose the local cues upon which to base an orienting strategy. This latter possibility is lent credibility by the results of Experiments 4 and 5, which provided some tentative evidence that rats with lesions of the hippocampus are not as good as controls at discriminating between short and long walls. This discrimination is essential to both learning based on information provided by the shape of the environment, and the subsequent use of the strategy which is learned. If the hippocampus is indeed required for the distinction of long and short, it should be of little surprise that the loss of this system prevented rats from using an existing strategy based on the identities of the walls.

CHAPTER FOUR

EXPERIMENT 7

The experiments presented so far give several demonstrations that animals are able to use information provided by the shape of a solid-walled arena to navigate. As reviewed in Chapter 1, a number of studies have shown that animals are also able to use information derived from shape when that shape is composed of discrete landmarks rather than solid walls. Greene and Cook (1997) trained rats to find food by referring to an array of distinctive landmarks, before exchanging them for novel ones. Despite this change, rats' preference for searching in particular areas of the arena was preserved. Since the identities of the landmarks had changed, rats' search behaviour must have been governed by some aspect of their arrangement.

Benhamou and Poucet (1998) also showed that rats were able to find a hidden goal based on an array of landmarks. Rats were trained to find a hidden platform in a watermaze, whose position was specified by the location of a triangular array of identical landmarks. Rats quickly learned to search in the area of the pool in which the platform was located, a result which Benhamou and Poucet attribute to their use of the shape of the array for orientation. Both these authors and Greene and Cook (1997) suggest that rats' use of discrete landmarks to find a hidden goal is indicative of the presence of a global representation for processing shape information. In the introduction to this thesis, however, I argued that these results could be explained by assuming that animals used local rather than global cues to find the goal (for a fuller consideration of these issues, see Chapter 1).

This idea was tested by Esber et al. (2005), who trained rats to find a platform in a watermaze containing a rectangular array of four identical cylindrical landmarks. The platform was hidden in one corner of the rectangular array, and rats learned to visit either that corner or the identical opposite corner more often than the remaining two. Following this training, rats were placed into a kite-shaped array consisting of the same four identical landmarks. The two most frequently visited corners in the kite-shaped array were the obtuse-angled corner and the right-angled corner which had the same geometric properties as the correct corner in the rectangle. On this basis, Esber et al. concluded that the rats located the platform in the rectangular array by using local information provided by the landmarks. In particular, an analysis similar to that applied to the transfer from rectangle to kite in Experiment 1 of this thesis suggested that the local cues used by rats were the short 'sides' of the rectangular array. The results were consistent with the idea that rats identified a pair of landmarks that were close together (i.e. a 'short side' of the rectangle) and learned which of these two landmarks the platform was closest to. In an attempt to confirm this suggestion, Esber et al. conducted a second experiment, during the first stage of which rats were trained to find a hidden platform in the same rectangular array of landmarks used previously. A test trial was conducted with two of the four landmarks removed from the pool; a short 'side' of the array remained. Rats swam to the end of this side which matched the platform's previous location in relation to the short sides of the rectangular array. The short sides, then, seem to be capable of supporting a preference for correct over incorrect corners in a rectangular array of landmarks.

This method of locating the platform, by referring to a single side of the shape, is similar to the strategy adopted by rats in a solid-walled shape (as demonstrated in both Experiment 1 here and by Pearce et al., 2004). It is possible that these two types of navigation progress in the same manner. If this is the case, hippocampal lesions should affect the ability of rats to navigate in an array of landmarks in the same way as they affect navigation in solid-walled shapes. As shown by the results of Experiment 1, rats with damage to the hippocampus are impaired at using this type of information when it is provided by a solid shape. They are not impaired, however, at using feature information. In Experiment 7, I investigated whether this dissociation between the ability to use geometric and feature information following hippocampal lesions is also present in a paradigm in which the local information is provided by the shape of an array. It is also worth noting that O'Keefe and Nadel's (1978) cognitive mapping theory predicts that rats with hippocampal lesions should be impaired at using an array of discrete landmarks to navigate.

Hippocampally-lesioned rats (the hippocampal group) and controls (the sham group) were trained to locate a hidden platform in one corner of a rectangular array of landmarks similar to that used by Esber et al. (2005). Two versions of this task were carried out: the first was designed to find out whether rats with hippocampal lesions were impaired at locating the platform in this array when feature information was available, while the second stage assessed their performance in the absence of features. In the first stage, two of the cylindrical landmarks were black and two were grey (Figure 45, top panel). Animals were trained to find the platform in a similar manner as for previous experiments, with the platform located in either corner A or corner C for half the animals and either corner B or corner D for the other half. The landmarks in the correct corners were always black. For the second phase, feature information was removed by the replacement of the grey landmarks in the incorrect corners with two more black landmarks (Figure 45, lower panel). If navigation in this

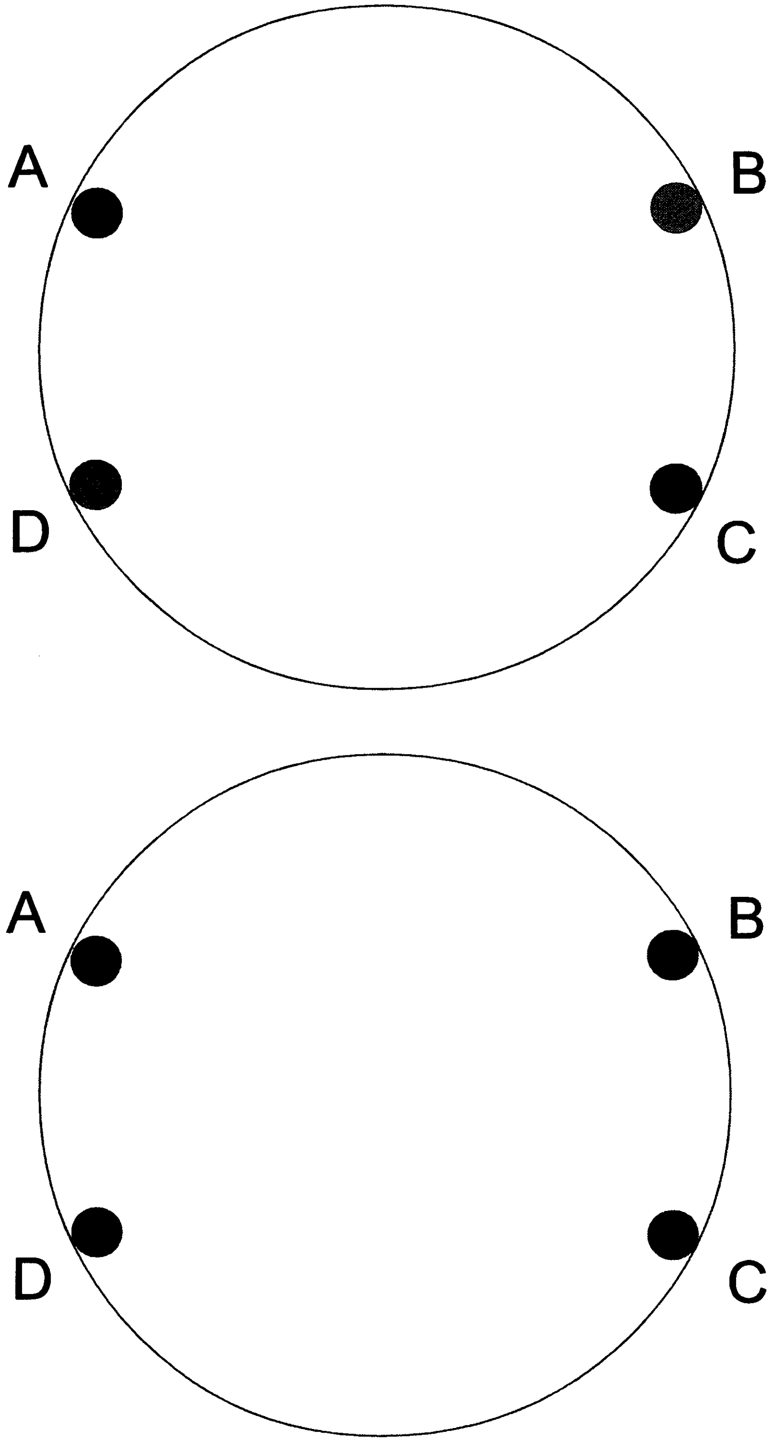

Figure 45. The two arrangements of landmarks used during Experiment 7. Animals were trained with two rectangular arrays of landmarks, one of which was composed of two black landmarks and two grey landmarks (top panel), and one of which was composed of four black landmarks (lower panel).

rectangular array progresses according to the same mechanisms as navigation in the solid rectangle, then the hippocampal group should show an impairment in this stage.

If the hippocampal rats do indeed show an impairment when the feature information is removed, there are two possible explanations. The first is that these rats are inferior to controls at location of the platform in the absence of features; the second, more mundane, explanation is that the general performance of the lesioned animals is subject to a deterioration over time. To rule out this latter explanation, all rats were given three additional training sessions with feature information present. If the hippocampal group show no impairment here, we will be able to conclude forcefully that the hippocampus is required for the use of shape information but not features in this type of array.

Method

Subjects and apparatus. The subjects were 16 male rats from the same stock and housed in the same manner as for previous experiments.

Four cylindrical landmarks were used to create each rectangular array. Each cylinder was 14.5 cm in diameter and 120 cm high. Each landmark extended 91 cm above the surface of the water. Landmarks were placed against the pool wall, and arranged so that they formed a rectangular array measuring 1.8 × 0.9 m. To make the black and grey array, two landmarks were coloured black while the remaining two were coloured grey. Opposite pairs of landmarks were always the same colour. To make the black array, all four cylinders were black. Details that have been omitted were the same as for previous experiments.

Experimental procedure. Rats were taken to the test room in groups of four. Both groups received four sessions of pretraining in a circular watermaze, during which animals were required to locate the platform, which had the beacon attached to it. During sessions 5-28, rats were trained to locate the platform in the black and grey array. The centre of the platform was located 25 cm from the centre of the nearest cylinder, on a line that bisected the corner of the rectangle. For half the rats the platform was located in either corner A or corner C, and for the other half it was located in either corner B or corner D. The cylinders in the incorrect corners were coloured grey. The beacon was attached to the platform for sessions 5-9.

Following this training, rats were trained in a similar manner in the black array during sessions 29-39. They were then trained during sessions 40-42 in the black and grey array. Procedural details that have been omitted were the same as for previous experiments.

Results

Figure 46 shows reconstructions of the maximum (light shading) and minimum (dark shading) extent of the hippocampal lesions on horizontal sections taken at various distances in mm ventral to the surface of the brain (top to bottom: -3.1, -3.6, -4.6, -5.6, -6.6, -7.6, -8.4 mm). One rat from the hippocampal group was excluded from the following analyses because of insufficient cell loss in the hippocampal region (less than 50 %). The remaining rats sustained cell loss of between 75 % and 100 %. In the following analyses, the hippocampal group contained only seven rats.

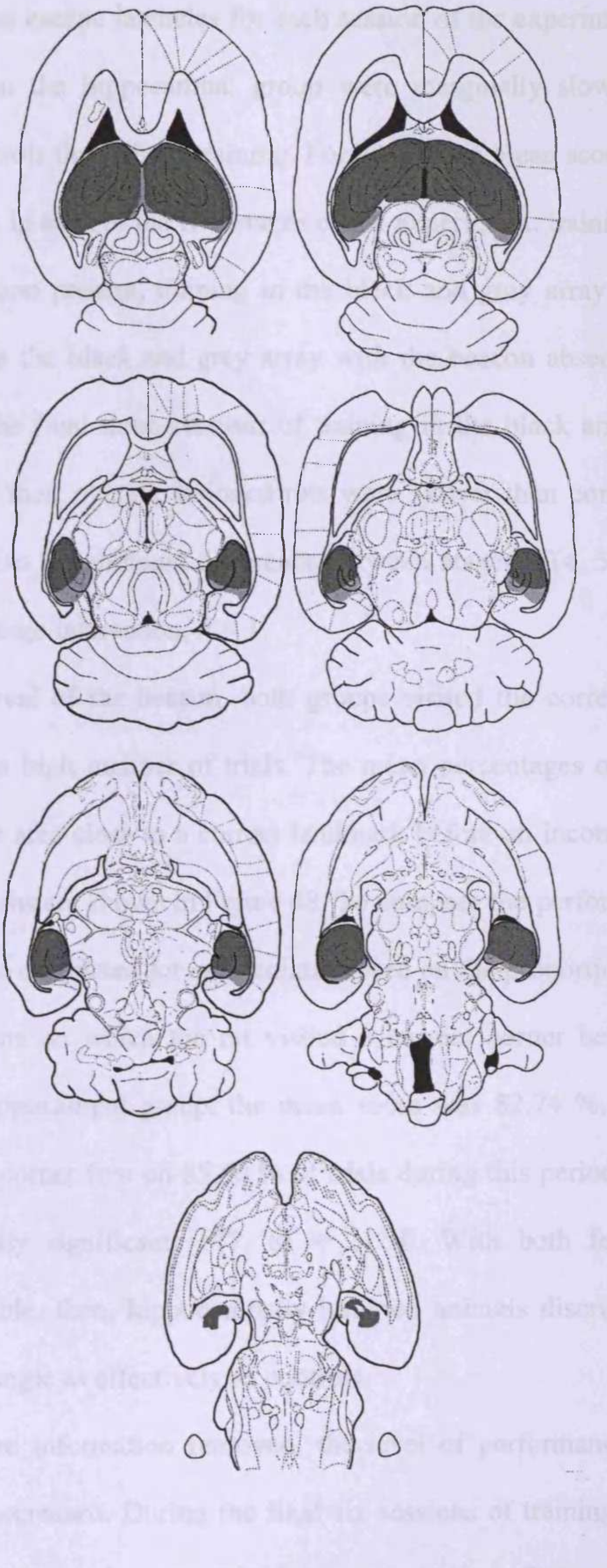

Figure 46. The maximum (light shading) and minimum (dark shading) extent of the hippocampal lesions for Experiment 7.

Group mean escape latencies for each session of the experiment are shown in Figure 47. Rats in the hippocampal group were marginally slower to locate the platform than controls throughout training. For each rat, a mean score was calculated for all the sessions in each of the five stages of the experiment: training in the circular pool with the beacon present, training in the black and grey array with the beacon present, training in the black and grey array with the beacon absent, training in the black array, and the final three sessions of training in the black and grey array. An ANOVA revealed that, overall, lesioned rats were slower than controls, $F(1, 13) = 8.98$. There was also a significant difference between stages, $F(4, 52) = 18.38$; there was no Lesion × Stage interaction, $F < 1$.

After removal of the beacon, both groups visited the correct corners of the rectangle first on a high number of trials. The mean percentages of trials on which animals visited the area close to a correct landmark before an incorrect landmark for each of these sessions are shown in Figure 48. To compare the performance of the two groups, scores were calculated for each animal based on the proportion of trials during the last six sessions on which the rat visited a correct corner before an incorrect corner. For the hippocampal group, the mean score was 82.74 %, while sham rats visited the correct corner first on 85.60 % of trials during this period. This difference was not statistically significant, $U(7, 8) = 21.50$. With both feature and shape information available, then, hippocampally-lesioned animals discriminated between corners of the rectangle as effectively as controls.

With feature information removed, the level of performance shown by the lesioned animals decreased. During the final six sessions of training with four black landmarks, the hippocampal group visited the correct corner first on only 62.50 % of trials, while the sham group chose one of the two correct corners first on 91.67 % of

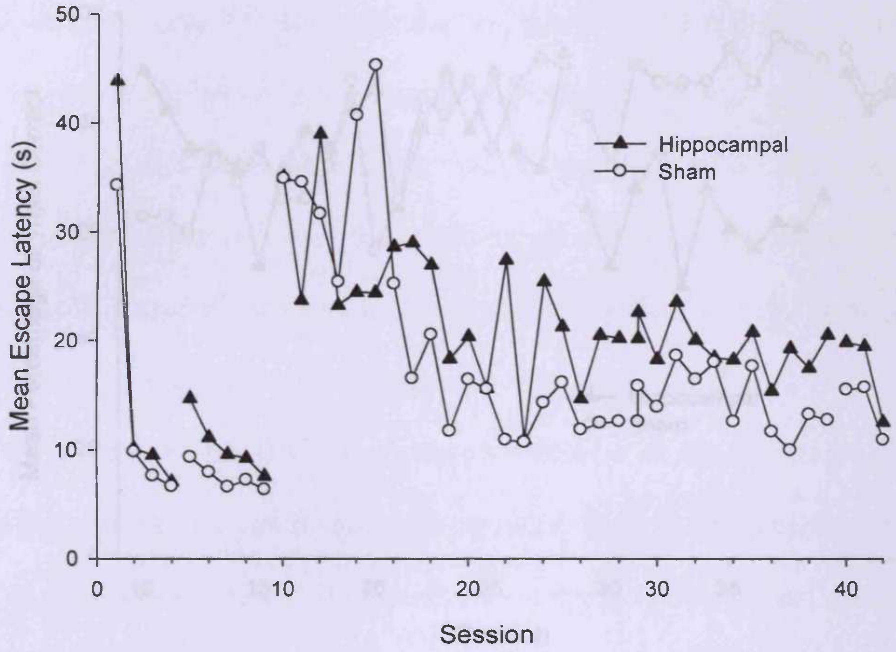

Figure 47. Mean escape latencies for the two groups of Experiment 7. Sessions 1-4 were conducted in the circular pool with the beacon attached to the platform; sessions 5-9 were carried out with black and grey landmarks and the beacon present; sessions 10-28 were carried out with black and grey landmarks present but no beacon; sessions 29-39 were conducted with four black landmarks; sessions 40-42 were carried out with two black and two grey landmarks, as for sessions 10-28.

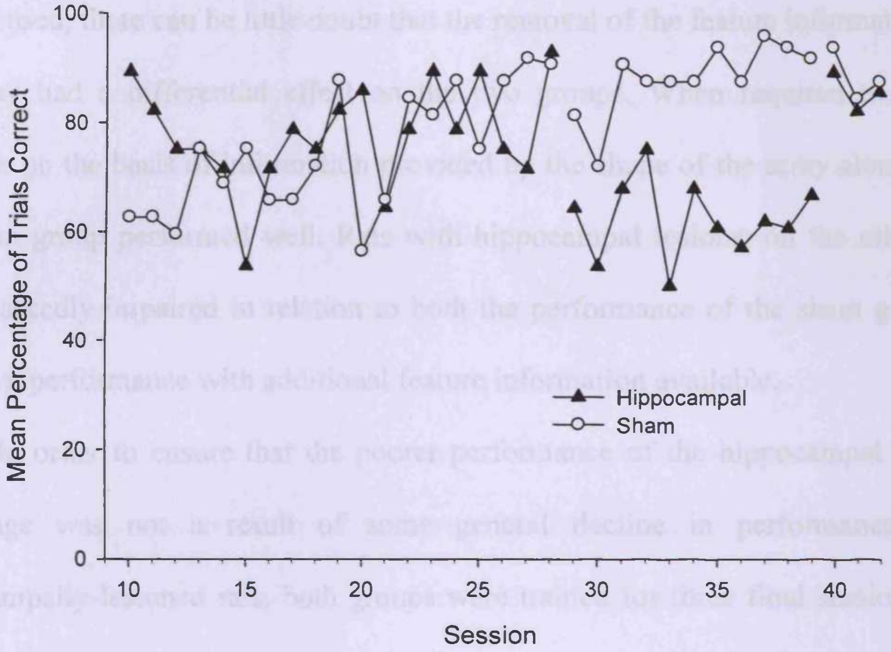

Figure 48. The mean percentage of trials on which rats in Experiment 7 approached a landmark in a correct corner of the array before an incorrect corner. Sessions 10-28 and sessions 40-42 were carried out with black and grey landmarks; sessions 29-39 were conducted with four black landmarks.

trials. The two groups' scores differed significantly, *U*(7, 8) = 5.00. Furthermore, a binomial test revealed that the level of performance in the hippocampal group was not above chance. While this could feasibly represent an insensitivity of the statistical method used, there can be little doubt that the removal of the feature information from the array had a differential effect on the two groups. When required to find the platform on the basis of information provided by the shape of the array alone, rats in the sham group performed well. Rats with hippocampal lesions, on the other hand, were markedly impaired in relation to both the performance of the sham group and their own performance with additional feature information available.

In order to ensure that the poorer performance of the hippocampal group in this stage was not a result of some general decline in performance of the hippocampally-lesioned rats, both groups were trained for three final sessions in the original array of two black and two grey landmarks. During these three sessions, the hippocampal group visited a correct corner first on 85.71 % of trials; for the sham group, this score was 88.54 %. The two groups did not differ, *U*(7, 8) = 24.50. This reinforces the idea that lesioned animals were able to locate the platform just as effectively as controls in the presence of feature information.

The pattern of results here is similar to those obtained in solid-walled shapes. While rats with hippocampal lesions are able to use feature information as effectively as controls, they have great difficulty in using information provided by shape. As already mentioned, there is evidence that navigation progresses according to local cues in both solid-walled arenas (Pearce et al., 2004; Experiment 1) and arrays of discrete landmarks (Esber et al., 2005). These similarities are suggestive of common mechanisms for the use of these two types of environment.

Skov-Rackette and Shettleworth (2005), however, have suggested that arrays of objects are not processed in the same way as solid-walled shapes. In a series of experiments, rats were allowed to explore an open field containing a landmark array. Typically, the amount of exploration behaviour shown by the rats decreased with prolonged exposure. If a change was made to the array, the animals responded by reinstating exploration of the objects which had moved. In one experiment, for instance, rats were allowed to explore a square array of four landmarks before one of these landmarks was moved to a location further from the centre of the square. After this transformation, rats spent more time exploring the landmark which had moved than any other. In another test, rats were allowed to explore a triangular array of objects. The objects were then rearranged, so that the new array was a mirror image of the old one. When placed into an open field with the new array, rats did not show any renewal of exploration. This, the authors suggested, was because the animals were not sensitive to the change in the array. On this basis, they argue that rats were not able to distinguish between landmark arrays on the basis of 'sense', a geometric property which allows a cue or configuration of cues to be distinguished from its mirror image. They argue, however, that in a solid-walled rectangle (e.g. Cheng, 1986) rats are able to learn sense relations to distinguish between mirror images of corners – otherwise they would be unable to learn to search in particular corners of a rectangular arena and not others. This difference between shapes composed of surfaces and shapes made up of landmarks is consistent, they claim, with the idea that learning based on these two types of shape does not proceed according to the same principles.

There are two reasons why accepting this analysis is problematic. The first is that rats are able to learn to visit one pair of corners in a rectangular array of landmarks more frequently than the remaining two (Esber et al., 2005; also

Experiment 7). According to the type of explanation offered by Skov-Rackette and Shettleworth for navigation in a solid-walled rectangle, this ability to discriminate between one corner and its mirror image in shape composed of discrete landmarks might indicate that rats are capable of learning sense relations in an array. The second problem is that, although both this result and the behaviour of rats trained to locate a hidden goal in one corner of a rectangle show rats discriminating between one corner and its mirror image, we have no indication that learning progresses according to relational information incorporating sense. Rather, rats may locate the platform by learning based on a single cue such as a wall. This idea is supported by the analyses of transfer tests offered by Esber et al. (2005), Pearce et al. (2004), and in this thesis (Chapter 2). This type of learning does not require animals to learn about the spatial relationship between elements of a corner, or to distinguish between corners on the basis of their spatial relationships among elements – animals need only to learn to search in a particular position in relation to a single cue. There is little evidence to suggest that sense information is encoded in either shapes composed of surfaces or landmark arrays.

It seems likely to me that, rather than possessing two distinct systems for the use of information provided by solid-walled shapes and landmark arrays, animals process the information provided by these two types of arena in a similar manner. Strategies for locating a hidden goal in both landmark arrays and solid shapes may be supported by learning about local cues, and in both cases learning in one environment may transfer to another environment which shares the critical local cues. Also in both cases, hippocampal damage impairs animals' ability to locate a hidden goal. These similarities are consistent with the idea that learning based on information provided by the two different kinds of shape progresses according to common local-cue mechanisms.

CHAPTER FIVE

EXPERIMENT 8

When rats are placed into an arena with a rectangular shape, they are able to locate a hidden goal according to information provided by the walls of the arena. They are able to do this even when the walls of the arena are featureless, and the rats must rely on information provided by shape alone (Experiments 1, 3, 6; Cheng, 1986; Hayward et al., 2003). Although a traditional explanation, as advocated by both Cheng and Gallistel (1990), is that this learning progresses according to global properties of the environment, the results of Experiment 1 and those obtained by Pearce et al. (2004) suggest that rats may learn to find the goal based on local cues provided by the shape of the environment.

There are two ways in which local cues may be used to discriminate between corners of a rectangle in this apparatus. The first of these possibilities is that rats learn about the configuration of walls at the corner containing the goal. Considering the rectangle in Figure 1, if the platform is located in corner A, animals may learn to approach corners in which a short wall is to the left of a long wall. Such a strategy would reliably lead to animals approaching corners A and C, and avoiding B and D. An alternative, and simpler, strategy is to learn about the position of the platform in relation to a single feature such as a wall. Suppose that animals learned the relationship between the platform's position and the nearest long wall; if the platform were located in corner A, the animal would learn to search at the left-hand end of the long walls. If the wall selected was AB, the animal would approach corner A; if the wall selected was CD, the animal would approach corner C. Corners B and D would not be visited by an animal using this strategy. These two methods based on local cues are both equally capable of accounting for the higher number of visits to corners A and C than B and D when the platform is located in a corner matching A and C.

Transfer tests were carried out by both Pearce et al. (2004) and in Experiment 1 here. In both these tests, rats were placed into a kite-shaped pool (see Figure 3). When placed into this arena, the two local cue accounts outlined above make differing predictions for rats' distribution of search behaviour. A strategy based on learning about corners of the rectangle should lead rats to predominantly visit the a corner with similar geometric properties to that which had previously contained the platform. To be clear, an animal trained to find the platform in corner A or C in the rectangle might be expected to visit corner E in the kite on the greatest number of trials because its configuration of walls matches corners A and C. A single-feature strategy based on the long walls of the arena makes a slightly more complex prediction for how animals will behave when placed into the kite, with the result dependent on the long wall in the kite that is selected for orientation. An animal trained to search at the left-hand ends of the long walls may search at corner E if wall EF is selected for orientation, but will search at corner F if the wall selected is FG. The results of transfer tests most closely resemble this latter pattern, with rats visiting the right-angled corner matching that which contained the platform in the rectangle, and the acute-angled corner F, with roughly equal frequency (Pearce et al.; Experiment 1). This presumably reflects a tendency for rats trained in the rectangle to learn to find the platform based on a single wall.

Although these results suggest that rats were able to locate the platform based on a single wall, they do not exclude the possibility that they also learned to find the platform based on the spatial arrangement of walls at the corners of the rectangle, with a strategy based on a single wall preferred when animals are subsequently transferred into the kite. This account cannot be discounted on experimental grounds, merely on the basis of Occam's razor; since the results can be explained by assuming that the rats learned to find the platform based on a single wall, there is no cause to entertain the notion that they also learned an additional strategy based on configural information at corners. The principal aim of the current study is to bring some experimental evidence to bear on this issue, by assessing the extent to which animals are able to discriminate between two corners created by features of different lengths.

Confirming the use of a strategy for locating a goal in one corner of a rectangular arena based on the relationship between lengths at that corner is somewhat problematic. Any training procedure which permits learning based on the relationship between walls at a corner will necessarily also permit the use of the individual lengths comprising that corner. If we train animals to approach a corner like corner A in the rectangle, we cannot be sure that they are looking for a corner where a short wall is to the left of a long wall – they may simply be learning about the position of the platform in relation to one or other of these constituent walls. Any attempt to render the latter strategy invalid (for instance, by changing the relationship between a wall and the goal from trial to trial) will also prohibit the use of the former strategy. For this reason, it is not possible to assess the use of a strategy based on the spatial arrangement of walls at a corner in the environments previously described.

Now consider the square arena shown in the upper panel of Figure 49. The walls of this arena are white, with black Perspex panels attached to the walls at two of the four corners. In each of these corners, one of the panels is twice the length of the other; in corner I, the shorter panel is to the left of the longer panel, and in the opposite corner K, the shorter panel is to the right of the longer panel. In this sense,

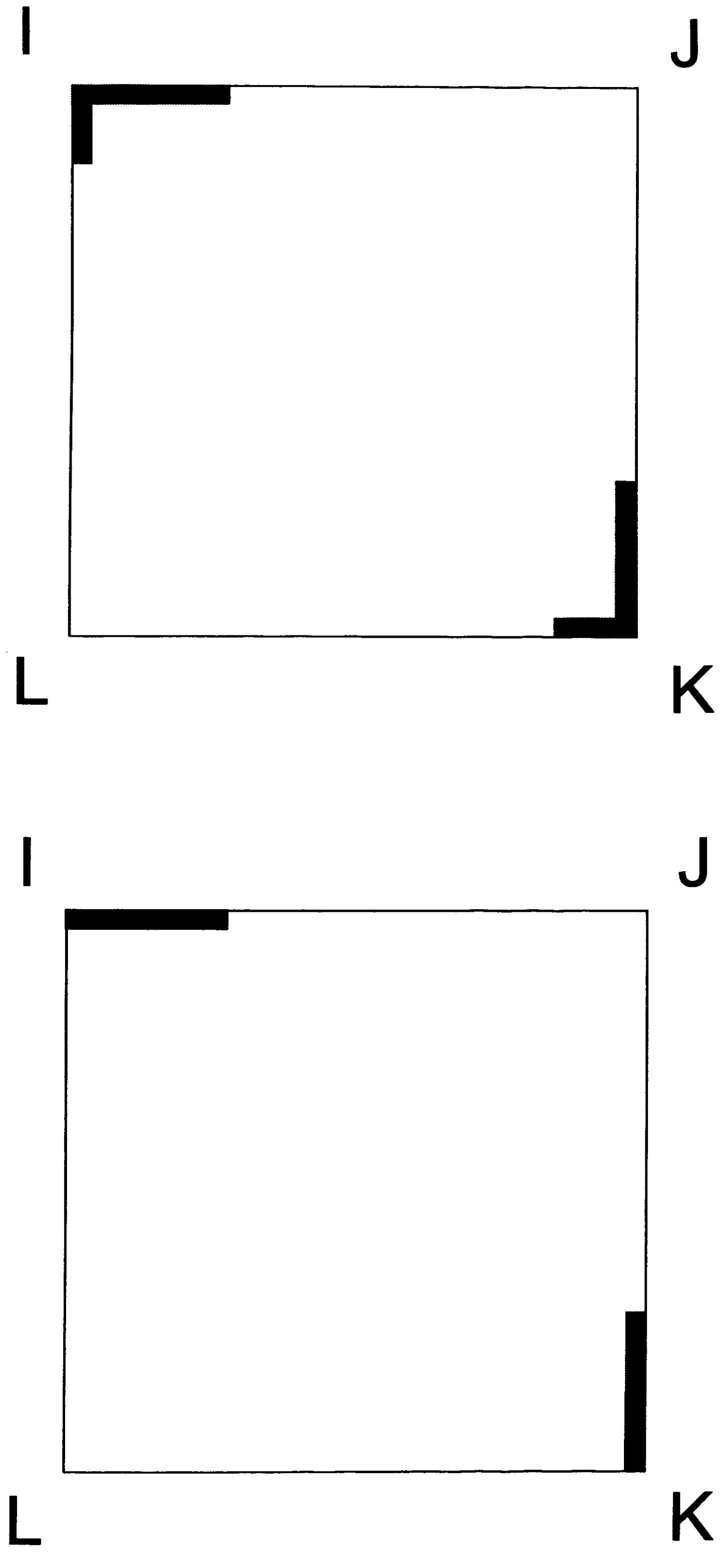

Figure 49. Schematic representations of the two test environments used in Experiment 8. Rats were trained with two black panels in each of corners I and K (top panel) before the removal of the shorter black panels. A long panel remained in each of these two corners (lower panel).

the panels in corner I have an arrangement similar to the walls of corners A and C in the rectangle, and corner K is akin to corners B and D. The task of distinguishing corners I and K in this square arena on the basis of their configurations of panels is similar to the task of distinguishing the two types of corner in the rectangle on the basis of their configurations of walls. One important difference between the two tasks is the availability of single-feature strategies. In the rectangle, corners A and C can be easily identified as being at the left-hand ends of the long walls; in the square arena shown in the upper panel of Figure 49, methods of discriminating between corners on the basis of single features are less obvious. One example of a single-feature strategy might be to visit corner I by searching for a corner in which the longer panel is located at the left-hand end of a wall rather than the right-hand end. Although such strategies are undoubtedly possible, this apparatus reduces the likelihood that animals will use them. If rats are able to discriminate between corners I and K in the square, it may be more credible to assume that this occurs because they are able to learn about a configuration of lengths at a corner.

Experiment 8 was conducted in order to assess the ability of rats to distinguish between the two arrangements of panels outlined above. Rats were trained to locate a hidden platform in a square swimming pool, with panels attached to the walls in the manner described above and the platform positioned near to one of the two corners containing panels. For ease of expression, this corner will be referred to as the correct corner and the opposite corner will be referred to as the incorrect corner. For initial sessions, a beacon was attached to the platform to assist learning. During training, performance was assessed by recording the proportion of trials on which the animals visited the correct corner without first visiting the incorrect corner. After completion of this training phase, the short panels were removed from the walls and training continued with only one panel present in each of the correct and incorrect corners (Figure 49, lower panel). This was done in order to assess the performance of the animals under conditions in which information about the configuration of lengths was not necessary for discrimination of corners; in this case, additional information about the relationship between colours at the corners could be used. In corner I, the white wall was visible to the left of the black panel, while corner K contained the reverse arrangement of colours.

If animals are able to use the configural information provided by these panels, they should learn to visit the correct corner more often than the incorrect corner. The alternative is that they will be unable to use this information, in which case they should visit these two corners equally. In the second phase of the experiment, a preference for the correct over the incorrect corner would suggest only an ability to use the configural relationship between the colours in these corners.

Method

Subjects and apparatus. The subjects were eight male Hooded Lister rats from the same stock and housed in the same manner as for previous experiments.

The square arena was constructed in the same way as for Experiment 5; panel inserts were also similar to those used in Experiment 5. Two of the inserts were 40 cm in length and two were 20 cm, all were 40 cm high and 2 mm thick. By positioning one board of each length in the corner of the square, an 'L' shape could be made, with two different arrangements possible (see Figure 49).

Procedure. Rats were transported to the room adjacent to the test room in groups of four. Each training session consisted of four trials, with rats allowed up to 60 s to locate the platform before being guided to it by the experimenter. Between each of the four trials, the square was rotated through 90 ° in a clockwise direction; for each trial in any given session, therefore, the square was in a different orientation. Rats were released from the mid-points of the four walls, facing the wall and with the four release points selected in a random order.

During all sessions, the inserts were positioned so as to create two 'L' shapes with differing arrangements at opposite corners of the square, I and K. The platform was located near to one of these 'L' shapes, and its location was consistent for each rat. For half the rats, the platform was located in corner I; for the other half, it was located in the opposite corner, K, which contained the alternative arrangement. The centre of the platform was 25 cm from the apex of the corner, along a notional line that bisected the corner. The platform was located in these positions for 21 sessions in total, with the beacon attached for the first 4 of these. For all trials within each of these sessions, the experimenter kept a record of which of the two corners with inserts the rat visited first upon release. A choice was considered to have been made when a rat's head entered an arc-shaped zone centred on each corner and with a radius of 40 cm; a choice in the corner containing the platform, therefore, indicated that a rat had passed within 10 cm of the platform's edge. After completion of this training, the shorter panels were removed from each corner and training continued as described above for an additional six sessions.

Results

Figure 50 shows the mean latencies during each session of the experiment. To compare the latencies from each stage, a mean latency was calculated for each animal for each of the three stages of the experiment (training with the beacon present, training with the beacon removed and two panels in each corner, training with one panel in each corner). These mean latencies were entered into a one-way ANOVA, which revealed a significant difference between the three stages, $F(2, 14) = 18.05$. Pairwise comparisons using a Bonferroni correction showed that the mean latency during each stage was different. Rats took longer to find the platform during the initial stage with the beacon attached than following its removal, and they took less time to locate the platform when only one panel was present in each of corners I and K than when these corners each contained two panels.

During the 17 sessions following removal of the beacon, rats were trained with two panels present in each corner. As seen in Figure 51, rats did not show a preference for searching in the correct rather than the incorrect corner during this stage. Animals visited the correct corner before the incorrect corner on only 56 % of trials during the last six sessions of this stage. A binomial test indicated that this performance was no different to that which might be expected by chance.

The results from the final stage, following removal of the shorter panels from each corner, show a different pattern. The percentage of trials on which the correct corner was entered before the incorrect corner showed a marked increase from the previous stage. During the six sessions of this stage, the correct corner was selected over the incorrect corner on 86 % of trials, with a binomial test showing this to be

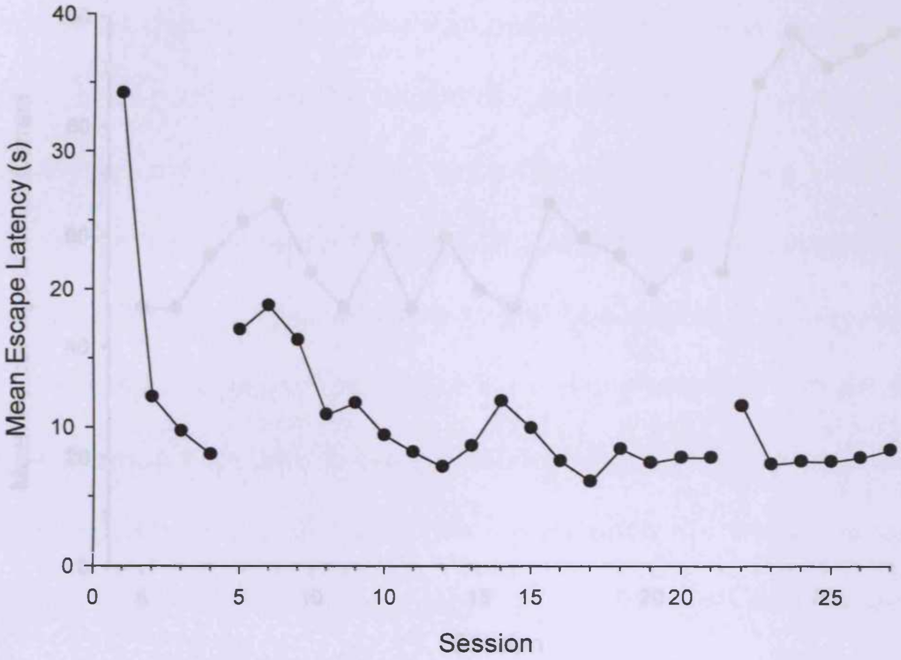

Figure 50. The mean escape latencies for each session of Experiment 8. Sessions 1-4 were conducted with the beacon attached to the platform, sessions 5-21 carried out with no beacon present and two panels present in each of the correct corner, and sessions 22-27 conducted following the removal of the short panels.

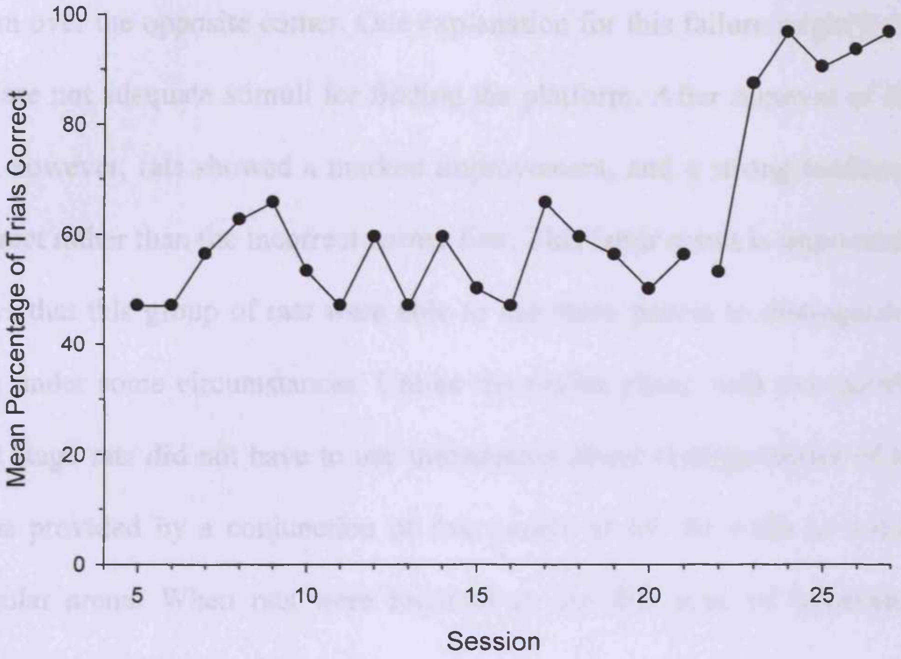

Figure 51. The mean percentage of trials on which rats visited the correct before the incorrect corner during each session following removal of the beacon in Experiment 8. Sessions 5-21 were conducted with two panels present in each of the correct and incorrect corners, while sessions 22-27 were carried out with the short panels removed.

higher than we might expect if the rats were choosing between these corners based purely on chance.

When two panels of differing lengths were present in each of the correct and incorrect corners, rats showed no preference for choosing the corner containing the platform over the opposite corner. One explanation for this failure might be that these panels are not adequate stimuli for finding the platform. After removal of the shorter panels, however, rats showed a marked improvement, and a strong tendency to visit the correct rather than the incorrect corner first. This latter result is important, because it shows that this group of rats were able to use these panels to distinguish between corners under some circumstances. Unlike the earlier phase with two panels, during the last stage rats did not have to use information about configurations of lengths of the type provided by a conjunction of two panels or by the walls at a corner of a rectangular arena. When rats were required to use this type of information, they demonstrated no ability to do so.

That the rats in Experiment 8 did not learn to discriminate the correct from the incorrect corner when two panels were present may reflect their inability to use configural information provided by conjoining surfaces of differing lengths. A rather more mundane possibility, however, is that rats may simply have difficulty perceiving the boundary between the two black panels. If this is true, each configuration of panels might be seen as a single panel, and the two arrangements may appear to be identical; discrimination of the correct from the incorrect corner would therefore be impossible. Another simple explanation for the results of Experiment 8 might be that rats cannot tell the difference between the long and the short panels. This would also presumably cause the two configurations of panels to appear identical, again making distinction of the correct and incorrect corners impossible. Experiment 9 was designed to test these two ideas.

EXPERIMENT 9

In Experiment 8, rats were unable to learn to visit the correct over the incorrect corner in the square arena shown in the top panel of Figure 49. One reason for this failure may be that rats are not able to use information about configurations of lengths to discriminate between two corners. Alternatively, they may have difficulty perceiving either the boundary between the two panels or the difference between the long and short panels. These alternative possibilities were explored in Experiment 9.

One group (the configuration group) was trained in a similar manner to the rats in Experiment 8. In order to decrease the likelihood of rats being unable to perceive the boundary between panels, Experiment 9 was conducted with a more readily visible boundary. To achieve this, the two panels in each of the correct and incorrect corners were separated by a small gap (Figure 52, top panel). A portion of the white arena wall was therefore visible between the two black panels. A preliminary study demonstrated that this gap was perceptible to rats (see Appendix).

To investigate the possibility that rats cannot distinguish the two lengths of panel, an additional group of rats (the length group) was trained in a similar manner but with only one panel present in each corner. In one corner of the square, a long panel was placed on the left-hand wall; in the opposite corner, a short panel was placed on the left-hand wall (Figure 52, lower panel). Rats were trained with a hidden platform located consistently in either the corner containing the long or the short panel, in a manner similar to that described previously. In this case, discrimination of the corners could only occur on the basis of the length of the panel in any given corner. If rats are able to reliably choose the correct over the incorrect corner, we will

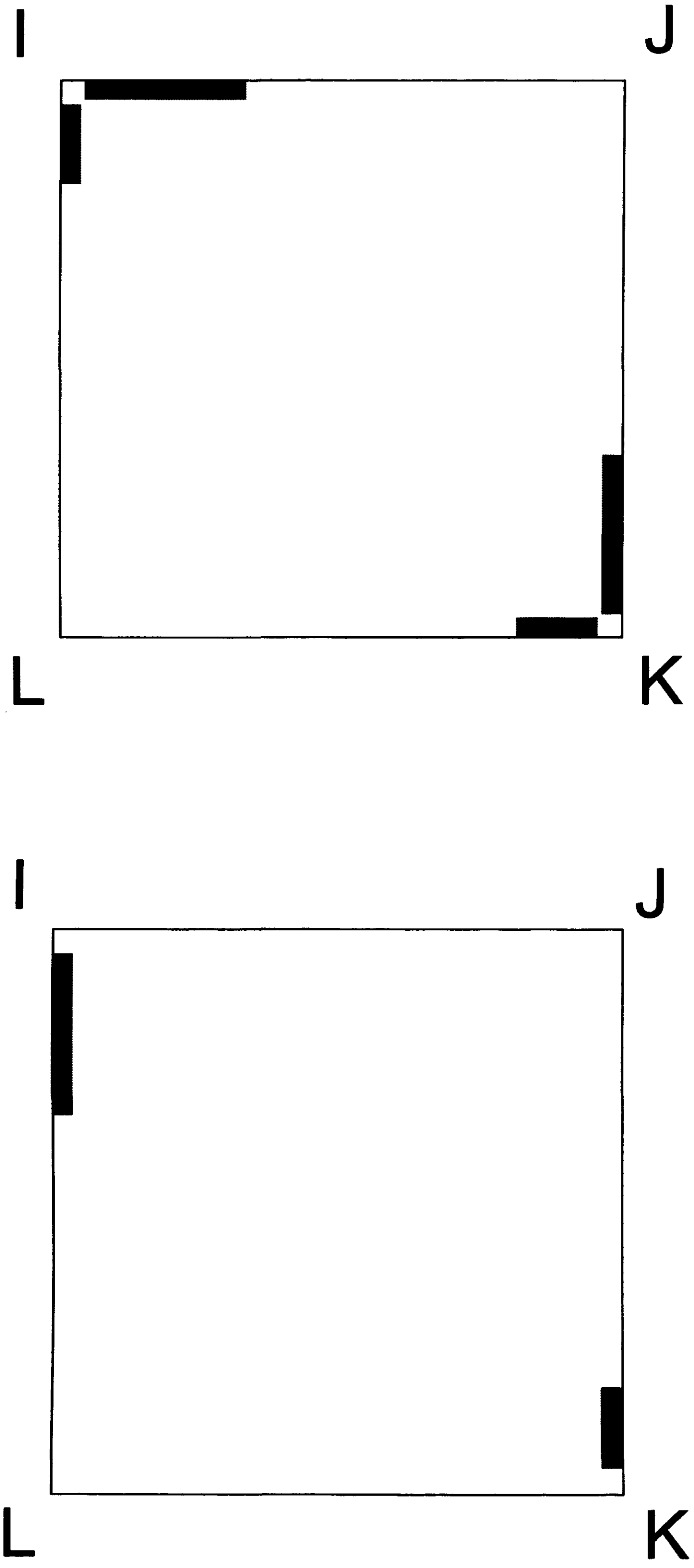

Figure 52. Schematic representations of the two square arenas in which rats were trained during Experiment 9. The configuration group were trained with two panels present in each of corners I and K (top panel), while the length group were trained with a long panel in corner I and a short panel in corner K (lower panel).

be compelled to conclude that these animals can distinguish the long from the short panels.

Method

Subjects and apparatus. The subjects were 16 male Hooded Lister rats, from the same stock and housed in the same manner as for previous experiments.

The apparatus was the same as for Experiment 8, with the same walls and panels used. In this experiment, all panels were positioned 2 cm from the corner of the square arena; therefore, when two panels were present in a corner, a 4 cm gap was visible between them. For rats in the configural group, two panels were present in each of two opposite corners. In one corner (corner I), a short panel was placed to the left of the corner and a long panel to the right; in the opposite corner (corner K), the short panel was to the right of the long panel. For rats in the length group, only one panel was present in each of two opposite corners. In one corner (corner I), a short panel was placed on the left, and in the other corner (corner K) a long panel was placed on the left.

Procedure. During 18 sessions, all animals were required to escape from the pool by swimming to a platform, which was located in one corner of the square arena. The platform was located in corner I for half the rats in each group, and in corner K for the remaining rats. The beacon was attached to the platform for the first 4 sessions of the initial stage. Session 19 consisted of three training trials of the type already described, and one test trial. During this trial, rats were placed into the pool in the absence of a platform and allowed to swim freely for 60 s. Their movement was monitored using

Watermaze Software. For the purposes of analysis, the pool was divided into four equal quadrants, and the amount of time each rat spent in each of these quadrants was recorded.

Procedural details that have been omitted were the same as for Experiment 8.

Results

Mean escape latencies for the two stages of the experiment are shown in Figure 53. For each rat, a mean latency across all sessions of each of the two stages was calculated. A two-way ANOVA of these scores revealed no difference between the two groups' latencies to find the platform, $F < 1$; latencies were significantly lower during the stage following removal of the beacon than when it was present, $F(1, 18) = 99.75$; and there was no Group × Stage interaction, $F(1, 18) = 1.21$.

The mean percentage of trials on which each group visited the correct corner before the incorrect corner during each session following removal of the beacon is shown in Figure 54. During the last six training sessions, the configuration and length groups visited the correct corner before the incorrect corner on 50 % and 63 % of trials respectively. A Mann-Whitney test using individual mean scores for these sessions demonstrated that this difference in performance was significant, $U(10, 10) = 17.00$; binomial tests showed that the configuration group performed at a level no different to that which might be expected by chance, while the length group performed significantly better than chance.

Following training, animals were given a test trial in their training environments. The amount of time spent during this trial in the quadrants adjacent to

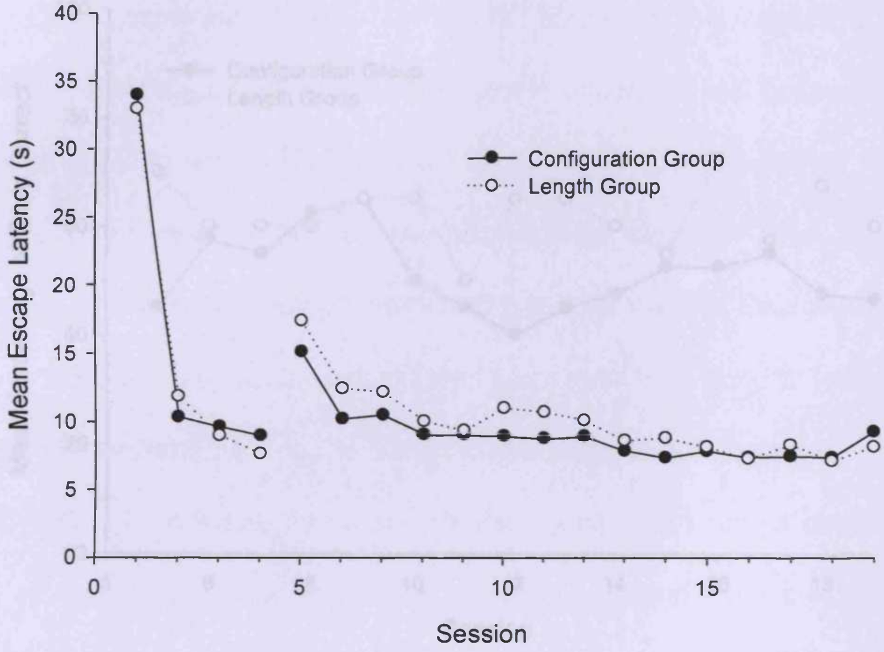

Figure 53. The mean escape latencies for the two groups of Experiment 9. Sessions 1-4 were conducted with the beacon attached to the platform, with the remaining sessions carried out with no beacon present.

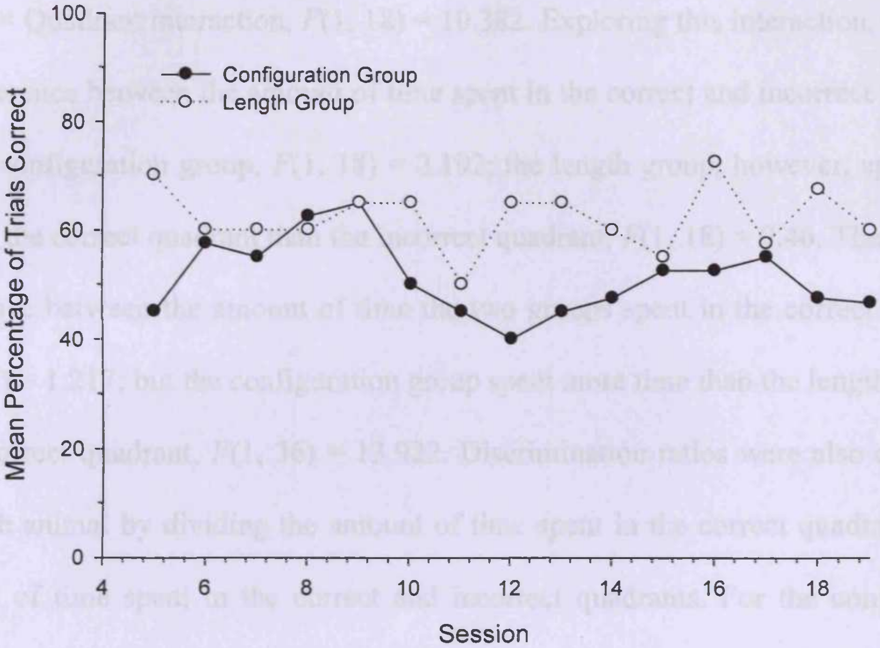

Figure 54. The mean percentage of trials on which rats visited the correct before the incorrect corner on each training session following removal of the beacon during Experiment 9.

the correct and incorrect corners was calculated, and these scores are shown in Figure 55; a two-way ANOVA on these scores revealed no overall difference between the two groups, *F*(1, 18) = 3.95; no difference between the overall amount of time spent in the correct and incorrect quadrants, *F*(1, 18) = 1.27; but there was a significant Group × Quadrant interaction, *F*(1, 18) = 10.382. Exploring this interaction, there was no difference between the amount of time spent in the correct and incorrect quadrants by the configuration group, *F*(1, 18) = 2.192; the length group, however, spent more time in the correct quadrant than the incorrect quadrant, *F*(1, 18) = 9.46. There was no difference between the amount of time the two groups spent in the correct quadrant, *F*(1, 36) = 1.217; but the configuration group spent more time than the length group in the incorrect quadrant, *F*(1, 36) = 13.922. Discrimination ratios were also calculated for each animal by dividing the amount of time spent in the correct quadrant by the amount of time spent in the correct and incorrect quadrants. For the configuration group, the mean score was 47 %, while for the length group this was 56 %. The length group were significantly better then the configuration group on this measure, *t*(18) = 3.32.

The configuration group were not able to learn to discriminate between corner I and K, as demonstrated by their poor performance during both acquisition and the test trial. Those rats trained with only one panel in each of two opposite corners were able to learn to visit the correct more than the incorrect corner, and spent more time searching near the correct than the incorrect corner during the test trial. These rats were not unable to use these cues to discriminate corners *per se*, but merely when the panels were arranged in such a way as to permit successful use of them only by taking account of their spatial configuration.

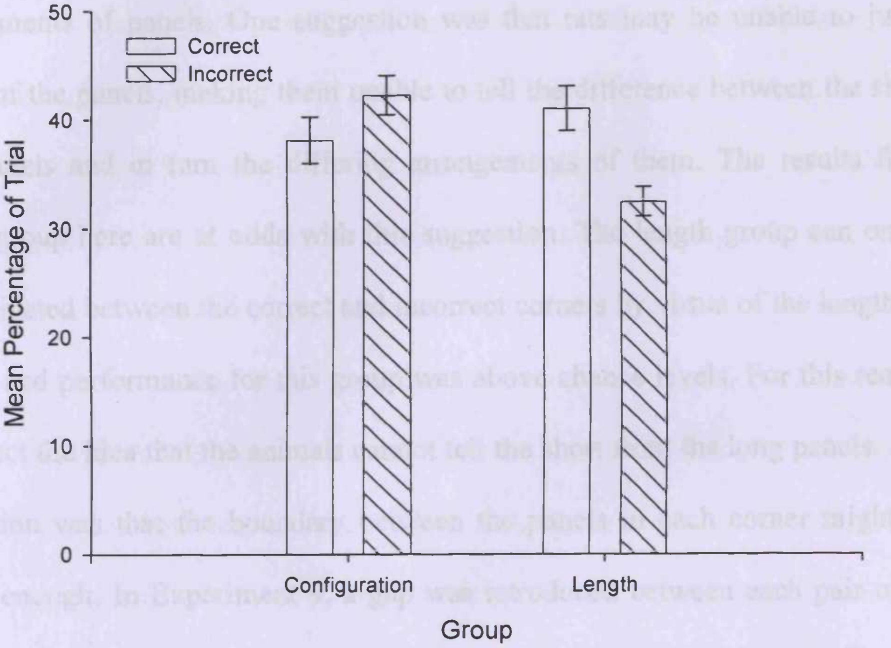

Figure 55. The mean percentage of the test trial carried out during Experiment 8 that was spent in the correct and incorrect quadrants of the square pool.

DISCUSSION

In the discussion following Experiment 8, I identified two possible simple explanations for the failure of rats in that experiment to discriminate between the two arrangements of panels. One suggestion was that rats may be unable to judge the length of the panels, making them unable to tell the difference between the short and long panels and in turn the differing arrangements of them. The results from the length group here are at odds with this suggestion. The length group can only have discriminated between the correct and incorrect corners by virtue of the lengths of the panels, and performance for this group was above chance levels. For this reason, we can reject the idea that the animals cannot tell the short from the long panels. Another suggestion was that the boundary between the panels in each corner might not be visible enough. In Experiment 9, a gap was introduced between each pair of panels presented to the configuration group, in an effort to increase the visibility of this boundary. Despite this, the configuration group was not able to discriminate between the correct and incorrect corners when two panels were present in each. This is again suggestive of an inability of rats to use the spatial arrangement of surfaces at corners to discriminate between them.

The presence of the white gap between panels for the configuration group was intended to make the boundary between panels more perceptible. One possible consequence of introducing this gap is that the white stripe may have been harmful to learning about the panels because the stripe may have acted as an overshadowing cue. In other words, rats in the configuration group may have failed to learn to use the panels to discriminate between corners because they attempted to find the platform on the basis of the white gaps. This strategy would be of no use for finding the platform, and it seems unlikely that it would have been adopted by the rats. Additionally, they did not learn to discriminate between the correct and incorrect corners in Experiment 8, where no gap was present. Although the idea that the stripe overshadowed learning about the panels in Experiment 9 is possible, the balance of evidence from the two experiments suggests that rats were not able to discriminate between the two configurations of lengths.

Experiments 8 and 9 were intended to assess rats' ability to discriminate between configurations of surface lengths. Although strategies for finding the platform based on single features were available, the method of placing panels within a square arena was intended to encourage the use of a configural local strategy. Rats failed to solve this task; they had great difficulty using local configural information when it was provided by these panels. The wider significance of this finding is that there is still no firm evidence of animals using this type of information at all, which calls into question the very idea that rats use the spatial relationship between cues for navigation in solid-walled arenas such as a rectangle. As previously stated, any behaviour consistent with the idea of a corner strategy being used in an environment with a distinctive shape must also be consistent with simpler strategies based on single features; and while there is clear evidence of animals using such single feature strategies to orient (Pearce et al., 2004), there is as yet no evidence which suggests learning based on corner configurations.

Our failure to demonstrate such learning also challenges the idea that rats possess mechanisms for navigation in environments such as a rectangular arena which are based on global information. The reason for this is the relationship between the different types of configural solution. One important feature of the types of strategy we have discussed here is that they fall into a natural hierarchy based upon the information required for their use. At the bottom of this hierarchy is the single wall strategy, which requires only that the animal learns the position of the goal relative to one wall. Suppose that the environment is the rectangle shown in Figure 1, and that the platform is located near to corner A. To use the single wall strategy, the animal must learn only about the position of the platform in relation to, say, wall AB. This would presumably require some mental representation of the length of this wall. At the next level of the hierarchy, the corner strategy must be based on information concerning two walls; in our example, these might be walls DA and AB. Once again, a mental representation is needed to code for the lengths of the walls and their relative positions. This representation must include all the information included in the representation of the lower level, single wall strategy. It is inconceivable that a representation could encode the position of the platform relative to walls DA and AB without also encoding the position of the platform in relation to each of the two constituent walls. This is the basis for the ordering of representations within the hierarchy. In a similar way, a global representation of the rectangle ABCD and the relative position of the platform is the highest level, since any representation capturing the platform's relations with all parts of the rectangle will necessarily contain information about the goal position relative to corners, and in turn to walls. The ordering of this hierarchy is not arbitrary; it is based upon the higher positioning of formally complex geometric representations which must logically include lower level, formally less complex ones. It is similar to the protocol used by Gallistel (1990) for organising geometries into a natural hierarchy.

The relevance of this hierarchical structure is that we have not been able to demonstrate the use of a corner strategy here – on the contrary, we have shown that rats have, at the very least, enormous difficulty using this type of information. This has clear implications for strategies placed higher in the hierarchy, i.e. those based on global representations. It is not possible for an animal to represent a goal location in relation to the overall geometric shape of the environment without also encoding its position in relation to the shape's constituent corners.

Of course, the relevance of Experiments 8 and 9 to this issue are dependent upon the use of the black panels attached to the walls of the arena being a result of the same mechanisms as navigation according to the shape of the environment itself. This is certainly not a given; in a distinctive shape, the relevant information is provided by the location of walls, whereas in Experiments 8 and 9 it is provided by landmarks. There is some evidence that these two types of cue may be learned about in different ways. Hartley, Burgess, Lever, Cacucci, and O'Keefe (2000) found that the firing of hippocampal place cells was controlled by an environmental boundary at a particular distance and direction from the animal. If this were the primary impetus for place cell firing, we might expect these cells to have a more active role when rats are required to learn about information provided by the shape of the arena than by landmarks, which suggests a possible disparity between Experiments 8 and 9 and earlier experiments conducted in distinctive shapes. This idea is supported by the difference in levels of performance seen in the results; specifically, that the level of performance seen when the location of the platform was indicated by panels fixed to the walls was lower than when the environment had a distinctive shape. However, while the evidence presented here that animals are unable to learn about the relationship of a goal to corners of a certain type is far from comprehensive, it is at the very least suggestive and poses a challenge to any view which supposes that navigation in distinctive shapes can be governed by higher level representations still. What is now needed is some clear indication that rats are able to use either geometric corner information or global cues to find a hidden goal. It is not easy to see how this information could be obtained.

CHAPTER SIX

GENERAL DISCUSSION

At the end of the introduction to this thesis, I outlined two principal aims of the work presented here. The first of these was to examine the way in which rats use information provided by the shape of the environment to find a hidden goal, and in particular to evaluate the claim that they use global properties of the environment to do so. The second aim was to assess the role of the hippocampus in these processes, global or local. In this final section, I will review the progress I have made towards these aims and attempt to place the results I have obtained into context with the existing literature.

How do rats use information provided by the shape of the environment to locate a hidden goal?

In the final two experiments of this thesis, rats were trained to find a hidden platform in one corner of a square arena with black panels attached to the walls (Experiments 8 and 9). These panels were arranged with a short panel on the left of a long panel in one corner of the square, and a long panel on the left of a short panel in the opposite corner. Rats did not learn to distinguish between these two arrangements of panels, perhaps because they are not able to use this type of relational information. These findings are in line with the results of Experiments 1 and 2, in which animals' behaviour after transfer from one environment to another was not consistent with the use of the relationship between surface lengths present in those environments.

The first two experiments contained in this thesis used a transformational approach to assess rats' use of local cues provided by the shape of an environment. In Experiment 1, rats were trained to find a hidden platform in one corner of a rectangular environment before being placed into a kite-shaped arena. When transferred into this new shape, rats most frequently visited the acute-angled corner of the pool or the right-angled corner with the same spatial arrangement of walls as the corner which contained the platform in the rectangle. I interpreted this as most closely resembling the pattern of results which would be expected if rats used the long walls of the rectangle to find the platform, and behaved in a manner consistent with this strategy when placed into the kite. In Experiment 2, rats were initially trained to find a hidden platform in one corner of the kite before being placed into a rectangular arena. Again, their behaviour after transfer was most consistent with rats' use of local properties to navigate in the original shape. The most common explanation in the literature for instances of animals orienting according to the shape of the environment is that they possess a global representation of their surroundings (Cheng, 1986; Gallistel, 1990). The results of Experiments 1 and 2, as well as the data presented by Tommasi and Polli (2004), challenge this point of view. At the very least, they are a convincing demonstration that animals do not rely solely upon strategies which involve matching the current environment to a remembered environment on the basis of shape congruence. In an effort to maintain a global account of navigation while explaining instances in which animals' behaviour transfers from an environment with a distinctive shape to an environment with a different shape, several recent articles have attempted to elaborate or modify the nature of the proposed global representation, in order to move away from the idea of congruence matching.

Gallistel (1990) was the first to suggest that a global representation of the environment may be based upon global shape parameters rather than the actual shape of the environment itself. One advantage of this approach outlined by Gallistel (and discussed in further detail by Cheng, 2005) is cognitive economy. A global representation based on shape parameters has the advantage of reducing the complexity of any representation that is formed, by excluding extraneous detail and storing a 'summary' of the overall shape. This reductive approach is economical in terms of storage, but less so in computational terms. Presumably, each time an animal enters an environment it must observe the entire space and perform this reduction, before the computed shape parameters for the current space can be compared with those stored in memory and a match can be found. According to this theory, an animal should be unable to behave in an appropriate environment-specific manner without first surveying the global shape and reducing it to a set of parameters. I am unable to say how likely this may be, although casual observation of animals in all of the experiments presented in this thesis suggest that they were able to swim towards the location of the platform immediately upon release into the pool, without any apparent need to look at the entirety of the shape surrounding them (a similar observation has been made by Tommasi, 2005). Reduction of the overall shape to a set of parameters, then, is advantageous for its economy in mnemonic storage but introduces a complexity in use that may not be borne out by the behaviour of animals.

Another advantage of this type of global representation suggested by Cheng is robustness, which he explained as follows:

> If the metric properties are measured approximately, almost always the case with biological systems, or if a small chunk of space is missed altogether, the computed [shape parameter] axes will be incorrect, but by a small margin. Contrast this with the local strategy of using a single conspicuous object as a pole

> for direction, the strategy of matching the feature properties of this conspicuous object. If one should make a mistake in matching, and pick an object to west rather than the correct one to the north, the error would be immense. (Cheng, 2005, in press).

It seems to me that this robustness must be closely related to the number of environmental elements encoded by the representation. Presumably, the rationale for supposing that these representations are robust is that a large number of elements of the shape are encoded, and that incorrect judgement of one or two of these is inconsequential - certainly in comparison to an erroneous judgement of a single critical feature. Logically, the most robust representation an animal could form would be based on the encoding of as many elements of the shape as possible. Such a representation would not only be robust, but it would allow an animal to discriminate between two very similar environments; it would, however, be costly. The economy of a spatial representation, as mentioned above, is dependent upon it having a simple nature when compared to the complexity of the environment it represents. Encoding a large number of elements means that the representation is less economical. A simple global representation might be able to do a reasonable job of summarising an environment while being cheap in terms of storage, but it necessarily discards information and so introduces the possibility of error. Local representations, however, can be both accurate and reasonably economical because they do not require the encoding of all the features of an environmental shape, merely those which are relevant to finding the goal. A global representation, by definition, encodes the entire environment – including information which is not relevant to the location of the goal. This cannot be considered to be economical.

Despite these shortcomings, global shape parameters have clear advantages in explaining the data presented in this thesis. Not only are they capable of accounting for the results of Experiments 1 and 2, they are also compatible with the results of Experiments 8 and 9. In these experiments, black Perspex panels were attached to the walls at the corners of a square arena, and rats were required to discriminate between two corners on the basis of those panels. Rats failed to discriminate between two different spatial arrangements of surfaces. I argued that it was not possible for a representation of the overall shape of the environment to fail to represent the arrangement of surfaces at corners, as this level of relational information is a prerequisite for a higher level of geometry (i.e. global geometry). Rats' failure to choose the correct corner over the incorrect corner in these experiments, I argued, was not consistent with the idea that they are able to learn the global shape of a rectangle. This discussion, however, was based on a conception of a global representation as a store of the overall shape of the environment, rather than a set of parameters which summarise that shape. It is not necessarily true that information about the arrangement of surfaces at a corner should be as readily accessible from a set of shape parameters which relate to the global shape of the environment, so animals that learn about the geometry of surfaces only in terms of this kind of mechanism might not be able to discriminate between the two different arrangements of surfaces used in Experiments 8 and 9.

Besides the principle of whether or not global parameters are notionally sound as a means for orientation, it is also necessary to consider whether the particular types of parameter suggested so far are suitable for explaining the data. Gallistel's (1990) choice was the principal axis of shape, a suggestion re-iterated by Cheng and Gallistel (2005). I have already considered the use of the principal axis, and on the basis of data reported by McGregor et al. (2005), I rejected this explanation. In fact, Cheng and Gallistel themselves have conceded that principal axes may not be adequate for accurate localisation of places. Some other type of global parameter, they say, may be more suitable for explaining the range of data relating to navigation by shape.

Cheng (2005, in press) has expanded upon the types of global shape parameter that he considers to be more capable of explaining spatial learning according to information provided by shape. In particular, he has focussed on symmetry axes and medial axes. Symmetry axes are similar in may cases to principal axes, but can curve to provide a more accurate representation of an irregular or curved space. This type of representation, however, suffers from many of the same limitations as one based on principle axes and is no more able to explain McGregor et al.'s (2005) results. More promising are medial axes, which take on a trunk-and-branch structure. This is applied to the shape in a relatively intuitive manner, summarising variations in width as well as length of an irregular shape. Protruding sections of an environment may be "given their own set of medial axes, and these sets are linked to the 'parent' space" (Cheng, in press). In other words, local areas of a space may be coded for by their own sets of axes, linking to other local axis sets within the same global environment.

This type of global representation may be capable of explaining McGregor et al.'s (2005) results, but only by matching local components of two different global sets of axes. Suppose, for instance, that the rectangular section of the pentagon shown in Figure 36 was given its own local set of axes within the pentagonal global space – in other words, if axes were applied to this rectangular section of the arena, and these axes were part of the set of parameters for the global environment. This local set would closely match the set of axes applied to the rectangular arena into which animals were subsequently transferred, and generalisation from one set to the other would lead animals to display the sort of behaviour shown by McGregor et al.'s rats when placed into the rectangle. The problem with this type of 'global' explanation for the transfer of behaviour is that it is not really global at all; it is a local matching account within a global framework. Rats using this type of representation would be reliant not upon the overall shape of the environment, but upon a particular portion of it which contained the goal. In order to provide an adequate explanation for the data while maintaining the idea of global processes, we are forced to return to the idea that animals use local information to find a hidden goal. Likewise, O'Keefe (1991) has provided further information about how a cognitive map might be used by animals; this conception permits the derivation of local information from a global representation, rendering the idea of a cognitive map essentially less global.

Throughout this thesis, I have argued that the idea that animals navigate with respect to a purely global representation of the environment is not supported by experimental evidence. Although this type of explanation is consistent with a great many results, these results can also be explained by appealing to explanations based on local strategies. Global explanations, meanwhile, are unable to account for some recent data without incorporating a local matching strategy of the kind described above. For these reasons, it is my view that the most promising explanations for instances in which animals orient with respect to information provided by the shape of the environment are those which assume the use of local information. For this view to be challenged, firm support for the existence of global representations is required.

What role does the hippocampus play in learning to navigate according to the shape of the environment?

In Experiment 1, I demonstrated that rats with hippocampal lesions were impaired at finding a platform hidden in one corner of a rectangular arena. A traditional explanation for this deficit might be that these animals are impaired because the hippocampus is the site of a global representation which ordinarily enables animals to find hidden goals in these types of environment (O'Keefe and Nadel, 1978). However, I have concluded that there is little evidence which demonstrates the existence of such a representation. In light of this, I have suggested that navigation in such environments proceeds according to local properties of the shape. If this is the case, it is important to consider why animals with lesions of the hippocampus are impaired in relation to controls on a local cue-dependent task. Several subsequent experiments were aimed at providing further information about the nature of the deficit seen following hippocampal lesions, in order to more fully understand the role of the hippocampus in orientation according to shape.

One possible explanation for the poor performance of rats with hippocampal lesions in a white rectangle was that they were not impaired at using the available cues *per se*, but that they were simply unable to learn to find a hidden platform in a watermaze. The results from groups trained in a black and white rectangle, however, suggested that they were not impaired at using information about the colour of walls to find the platform, merely the shape of the environment. The proposed method by which controls found the platform was by identifying a particular wall and swimming in a certain direction in relation to it; this ability was shown adequately by rats with hippocampal lesions in both Experiment 1 and Experiment 3 when there was some relevant information provided by the colour of the walls. In Experiment 3, when the black wall was not adjacent to the corner containing the platform, rats with hippocampal lesions still reliably visited the white corner which contained the platform before the white corner which did not.

On this basis, I concluded that rats with hippocampal lesions were impaired at selecting a wall and orienting according to that wall when the different walls in the arena could be distinguished on the basis of their lengths, but not when colour information was additionally available. I suggested two possible explanations for this deficit. The first was that rats with hippocampal lesions were unable to discriminate between long and short walls, and the second was that the hippocampus has some non-spatial role such as the modulation of cue salience (Rudy & Sutherland, 1995). Experiments 4 and 5 provided some tentative support for the former idea.

In fact, these two suggestions are not mutually exclusive. It is possible that rats with hippocampal lesions cannot tell the difference between the long and the short walls of the rectangle precisely because this discrimination requires hippocampal modulation of salience. According to Rudy and Sutherland (1995), the hippocampus is involved in discriminations involving configurations of cues because it amplifies the salience of relevant conjunctions of cues. This is particularly important, they suggest, when the to-be-discriminated cues are similar. If this is correct, we would expect the effect of the hippocampal lesions to be greatest when animals are required to choose between similar elements of an arena, rather than those which are very different. In Experiment 1, for example, it is surely true that a long black wall and a short white wall are less similar than a long white wall and a short white wall; the result being that finding the platform in the white rectangle should be more dependent upon the influence of the hippocampus than finding the platform in the black and white rectangle.

A similar argument can be applied to the results of Experiment 7, in which rats with hippocampal lesions were impaired at finding a hidden platform in one corner of an array of landmarks when they were all black, but unimpaired when two of the landmarks were grey. The method for finding the platform which I have suggested animals used was that they located a pair of landmarks which were close together rather than far apart, and then searched near either the left- or the right-hand landmark of the pair. In order to use this strategy, animals were required to discriminate between pairs of landmarks, in order to select a pair that was close together rather than further apart. When four black landmarks were present, the landmark pairs to be discriminated were more similar than when two of the landmarks were grey, which should mean that the influence of the hippocampus is not as important.

One interesting prediction arising from this account is that the involvement of the hippocampus in the location of a platform in a white rectangular pool might be diminished if the ratio between the length of the long walls and the length of the short walls was increased. In other words, if the hippocampus is required for the discrimination of walls that are similar, it might be less important if the walls of a white rectangle are made less similar by increasing the difference in length between them. In the watermaze, this is not as easy to achieve as it might first appear. The restrictions of the circular pool in which the rectangle is constructed mean that the ratio between the long wall lengths and the short wall lengths cannot be increased by only lengthening the long walls; this must be accompanied by an additional shortening of the short walls. Such an alteration would introduce difficulties in assessing rats' corner choices, as the distance between a correct corner and an incorrect corner located at opposite ends of a short wall would be reduced. McGregor et al. (2005) used a rectangular test space with shorter walls, and found distinction of choices at the corners bounded by these short walls problematic. For this reason, I did not attempt to test animals in such a space. An alternative method would be to use a larger circular pool, but this apparatus was not available. An additional possibility might be to use an alternative method of testing, such as using a dry maze in which animals are required to find food hidden in some corners of a rectangle and not others – much like the apparatus used by Cheng (1986). This seems like the most viable option, and the results of an experiment conducted in this way would be undoubtedly informative.

A hippocampal mechanism based on enhancing salience is consistent with the results of Experiment 6. In this experiment, rats were trained to find a hidden platform in a white rectangle and a black and white square, and the effect of hippocampal deactivation in each was assessed. Test trials indicated that hippocampal deactivation caused an impairment in navigation in the white rectangle, but not the black and white square. If the walls of the white rectangle are more similar than the walls of the black and white square, the hippocampus should be critical for navigation in the white arena. According to the explanation just given, this is because the cues which are present here are similar, and their discrimination requires the alteration of salience provided by the hippocampus. When the hippocampus was deactivated, the system for raising the salience of the relevant features became unavailable, so it is not surprising that this treatment resulted in a deficit in using those cues.

In summary, I have demonstrated that hippocampal damage impairs the ability to use some, but not all, local cues. Although this deficit could be a result of some role for the hippocampus in the modulation of cue salience, this idea is relatively untested in this thesis and needs examination. What is clear is that hippocampal lesions resulted in marked deficits on local cue-dependent tasks, a finding which forcefully demonstrates that the hippocampus is not involved in the use of information provided by the shape of the environment solely as the site of a global representation of space.

APPENDIX

PRELIMINARY EXPERIMENT, RELATING TO EXPERIMENT 9

In order to assess the visibility of a gap between panels such as that used in Experiment 9, rats were trained to discriminate between two configurations of panels, identical with respect to the relative positioning of the long and short panels except that one configuration was divided by a gap and the other was not. This apparatus is shown in Figure 56. At the corner containing the platform, a short panel was positioned on the left and a long panel on the right with both 2 cm from the corner of the square. The opposite corner also contained a short panel on the left and a long panel on the right, but with no gap between them. If rats are able to learn to approach the corner containing the gap more often than the corner containing no gap, we will be able to conclude that the gap between the panels was perceptible.

Method

Subjects and apparatus. The subjects were five male Hooded Lister rats, from the same stock and housed in the same manner as for previous experiments.

The apparatus was the same as for previous experiments, with the same walls and panels used. In this experiment, two panels were present in each of two opposite corners. In both of these corners, a short panel was placed on the left and a long panel on the right. For the corner containing the platform, the two panels were separated by a 4 cm gap identical to that used for the configural group of Experiment 9; for the other corner, there was no gap between the panels.

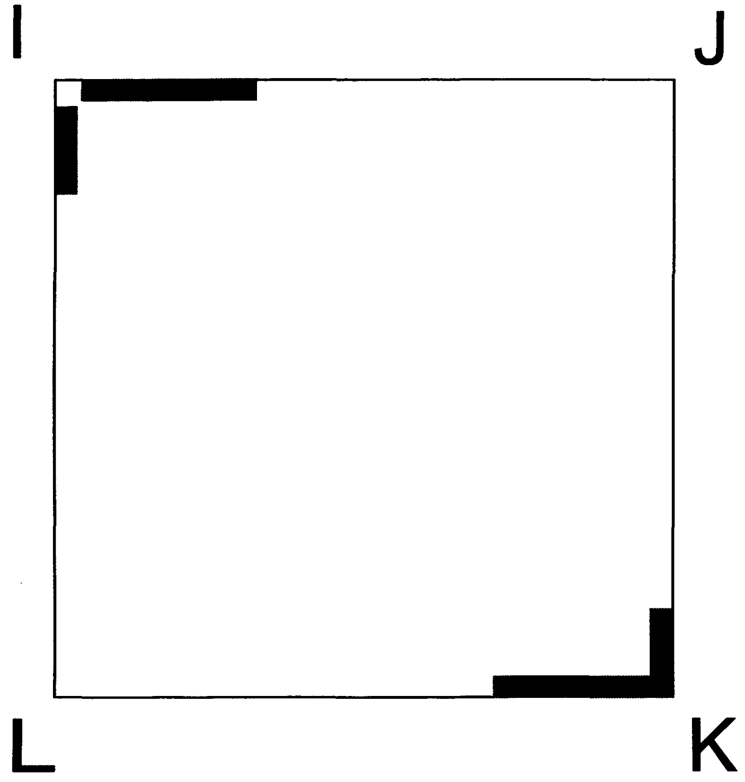

Figure 56. The square arena used for the preliminary study carried out prior to Experiment 9. Corners I and K both contain a short panel on the left of a long panel; in corner I these panels are separated by a gap, while in corner K there is no gap.

Procedure. Rats were trained for 15 sessions in the same way as for previous experiments, with the platform located in the corner in which the panels were separated by a gap. The beacon was attached to the platform for the first 5 of these sessions. On each trial, a record was made of which of the two corners containing panels was visited first. Procedural details that have been omitted were the same as for Experiment 9.

Results

Mean escape latencies are shown in Figure 57. A mean latency across all sessions of each of the two stages of the experiment was calculated; a within-subjects t-test on these scores revealed that rats took less time to find the platform during the stage following the removal of the beacon than when it was present, $t(5) = 6.67$. The mean percentage of trials on which rats visited the corner containing the platform before the opposite corner for each session following the removal of the beacon is shown in Figure 58. During the last six sessions, rats visited the correct before the incorrect corner on 63 % of trials; a binomial test revealed that this level of performance was significantly above that expected by chance.

Rats in this experiment successfully learned to approach the correct rather than the incorrect corner. Since the only difference between these corners was the gap between panels in the correct corner, we are forced to conclude that the gap was visible to rats. In light of this, it seems likely that the boundary between panels for the configuration group of Experiment 9 was visible.

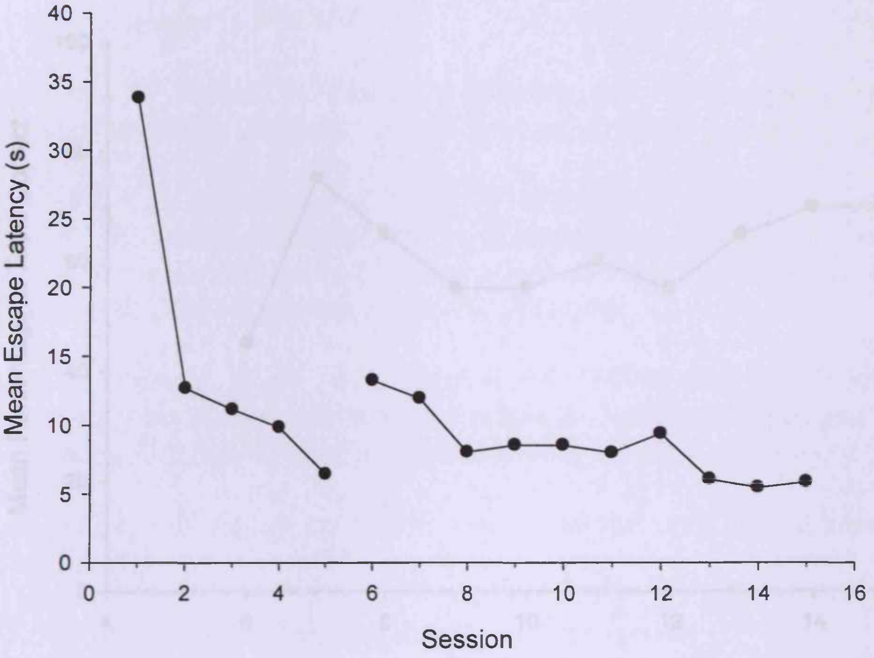

Figure 57. Mean escape latencies for each session of Experiment 10. Sessions 1-5 were conducted with the beacon attached to the platform, while sessions 6-15 were carried out in the absence of a beacon.

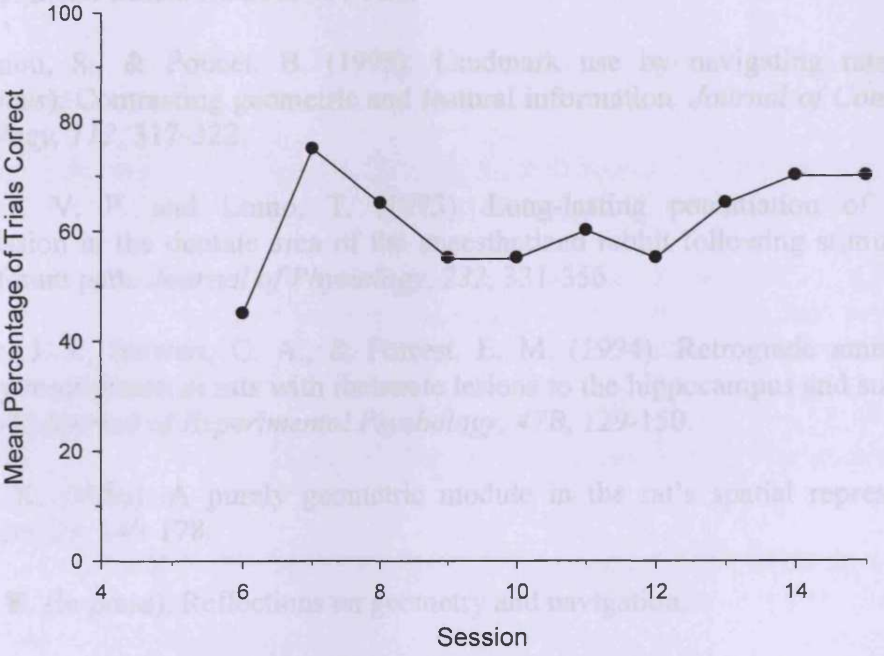

Figure 58. The mean percentage of trials on which rats in Experiment 10 visited the correct corner before the opposite corner following removal of the beacon.

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