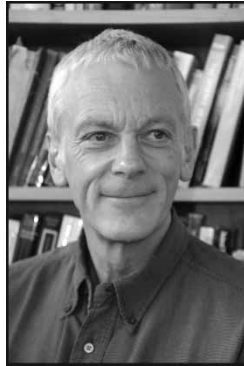


The 36th Sir Frederick Bartlett Lecture

An associative analysis of spatial learning



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The ability of animals to find important goals in their environment has been said to require a form of learning that is qualitatively different from that normally studied in the conditioning laboratory. Such spatial learning has been said to depend upon the construction of a global representation of the environment, and the acquisition of knowledge about the position of goals with reference to this representation is said to be unaffected by the presence of other cues or landmarks. To evaluate the first of these claims, experiments are described that investigated the extent to which the effects of training in one environment transfer to another. To evaluate the second claim, experiments are described that investigated whether cue competition effects normally found in conditioning studies can be found in spatial tasks. Overall, the results indicate that most of the phenomena of spatial learning can be explained by the principles of associative learning. The implications of the reported results for an understanding of the neural mechanisms of spatial learning are considered.

Keywords: Spatial learning; Geometric module; Cue competition; Cognitive maps.

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Animals as diverse as bees and humans display an ability for spatial learning, which allows them to find a hidden goal that is some distance from one or more landmarks. Ever since Tolman (1948) published his article entitled "Cognitive maps in rats and men", it has been acknowledged that the principles governing this type of learning may differ from those that govern associative learning. O'Keefe and Nadel (1978), for example, drew a clear distinction between a locale system within the brain, which is concerned with place learning, and a taxon system, which is concerned with stimulus-response learning. Cheng (1986) and Gallistel (1990) proposed that the brain contains a geometric module that is responsible for learning about geometric relationships within the environment; they further proposed that this learning was unaffected by the presence of non-geometric cues (see also Wang & Spelke, 2002, 2003). Finally, Doeller and Burgess (2008; see also Doeller, King, & Burgess, 2008) have suggested that learning about boundaries in the environment takes place incidentally, whereas learning about local landmarks is governed by an associative error-correction rule.

From the perspective of associative learning theory, however, there is no good reason to suppose that spatial learning will be governed by rules that do not apply to other types of learning. The principles of associative learning have been shown to be true across a wide range of species and in a variety of different contexts. Given this generality, it would then seem reasonable to expect them to apply to spatial learning. The main purpose of the present paper is to determine which of these points of view is correct. Is spatial learning special and governed by rules that do not apply to associative learning, or can spatial learning be understood completely by referring to what is known about the mechanisms of associative learning? In an attempt to answer these questions, the following discussion will review the results from a series of spatial learning experiments, but first, by way of background, a brief introduction to the basic principles of associative learning is provided.

The classic example of associative learning is the dog who salivates on hearing a tone that signals

food (Pavlov, 1926/1927). This response is said to be a consequence of the growth of an association between internal representations of the tone and food, and the strength of the response is said to be determined by the strength of the association—that is, the associative strength of the tone. Although there remains some dispute concerning the way in which events that enter into associations are represented (e.g., Pearce, 2008; Wagner, 2008), there is general agreement about the conditions that promote the growth of associations. Learning is held to be driven by an error-correction principle, which results in stimuli competing for the associative strength they acquire (e.g., Rescorla & Wagner, 1972). For example, if two stimuli signal the same reinforcer, then they will each gain half the associative strength they would acquire if they had individually been paired with the same reinforcer. In this instance, the presence of one stimulus is said to overshadow the other. It is also possible to imagine a situation in which the experience of two stimuli, A and B, together signalling a particular event, is preceded by training in which one of the stimuli, A, by itself is paired with the same event. As a result of this treatment, A will gain all the available associative strength during the first stage and leave none for B when it is subsequently introduced. B will thus be unable to enter into an association with the reinforcing event, and the presence of A is said to block learning about B. At a more general level, the competition for associative strength results in stimuli that are the best predictors of a reinforcer gaining more associative strength, and thus more control over behaviour, than stimuli that are relatively poor predictors of the reinforcer.

Cognitive maps and cue competition

When they argued in favour of the notion that animals navigate by means of cognitive maps, O'Keefe and Nadel (1978) identified several properties of maps that might influence the acquisition of spatial knowledge. One property is that for a map to be of maximum value it should incorporate information about new landmarks as soon as they

are added to an environment. An implication of this proposal is that if animals are trained to find a hidden goal with reference to one set of landmarks, and then a new set is added, they will learn just as readily about the new set as if the training with the original set had been omitted. In other words, it follows that spatial learning will not be susceptible to blocking.

In order to test this claim, Roberts and Pearce (1999) conducted an experiment based on the design summarized in Figure 1. Rats in a blocking group were trained in Stage 1 of the experiment to find a submerged platform, which was attached to a landmark—a vertical pole—in a circular pool of opaque water. The pool was 2 m in diameter and was surrounded by curtains. Once the rats had mastered this task by swimming directly to the platform whenever they were released into the pool, the curtains were then pulled open for the second stage of the

experiment. The training continued in the same manner as before for the blocking group, except that now animals could view the cues provided by the experimental room. According to the proposals of O'Keefe and Nadel (1978) the introduction of the cues provided by the experimental room will lead to them being incorporated into a cognitive map that includes information about the pool and the position of the platform. The Stage 2 training should therefore allow the room cues to gain control over searching for the landmark in the pool. A rather different prediction is made if spatial learning is governed by the principles of associative learning. During Stage 1, and throughout Stage 2, the landmark above the platform will be a reliable cue for finding the platform. The landmark will therefore block learning about the room cues in Stage 2 and prevent them from gaining control over searching for the platform. These contrasting predictions

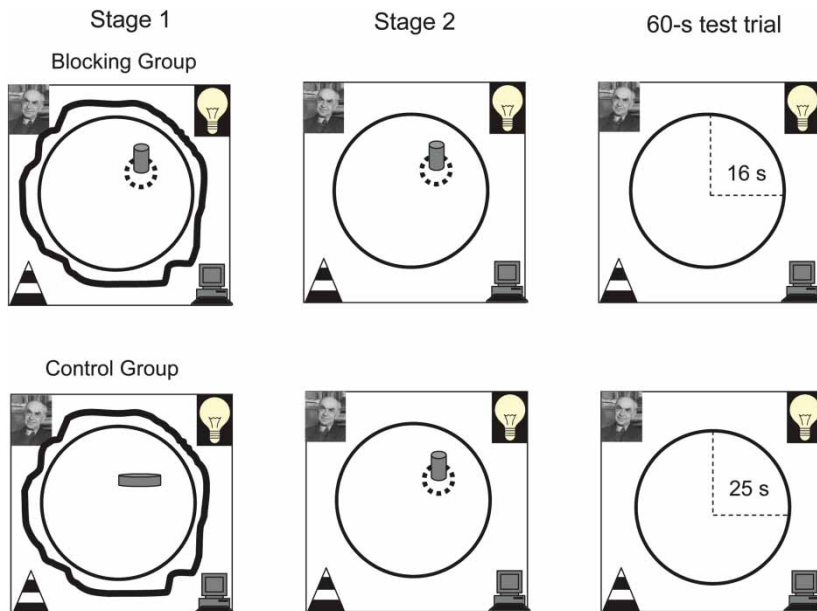


Figure 1. A plan of the apparatus used by Roberts and Pearce (1999) to study blocking of spatial learning. The large circle depicts a circular swimming pool; the small dotted circle depicts the location of a submerged platform. The filled objects within the pool depict a vertical rod attached to the platform (e.g., top left-hand panel) or a raised platform (bottom left-hand panel). The thick black line surrounding the pool depicts a curtain, and the objects in the corners of the room housing the pool depict landmarks. The numbers represent the amount of time that was spent during a 60-s test trial in the quadrant where the platform was originally located but which was absent for the test. To view a colour version of this figure, please see the online issue of the Journal.

were compared by means of a test trial in which both groups were placed in the pool for 60 s, again with the curtains open, but with the landmark and the platform removed. If the presence of the landmark did not block learning about the room cues, then rats would be expected to spend a considerable portion of the test trial in the quadrant of the pool where the platform was originally located. In contrast, if blocking had taken place then the room cues would be of no value for finding the platform, and rats should effectively search the pool at random and spend approximately 15 s in the correct quadrant. The results from the test trial, which are displayed in the top right-hand panel of Figure 1, were in keeping with the second of these predictions.

In order to demonstrate that the room cues can be used to find the platform within the pool, a control group was included in the experiment. This group was trained and tested in the same way as the blocking group, except that different landmarks were used within the pool during Stages 1 and 2. In Stage 1 the landmark was a visible platform raised 1 cm above the surface of the water, whereas for Stage 2 it was the same vertical pole above the submerged platform as for the blocking group. The new landmark at the outset of Stage 2 should have relatively low associative strength, and according to associative learning theory, there will be potential for this group to learn about the position of the platform relative to the room cues. The results from the test trial, see the lower right-hand panel of Figure 1, confirmed this prediction by revealing that the control group spent considerably more time than the blocking group in the correct quadrant of the pool. Other demonstrations of blocking of spatial learning have been reported by Biegler and Morris (1999), Diez-Chamizo, Sterio, and Mackintosh (1985), Redhead, Roberts, Good, and Pearce (1997), and Rodrigo, Chamizo, McLaren, and Mackintosh (1997). Thus it appears that animals do not automatically update their cognitive maps, if they form such maps, when stimuli are introduced into their environment. The next experiment was conducted in

order to test another property of cognitive maps that was predicted by O'Keefe and Nadel (1978).

Cognitive maps and landmark stability

Maps typically represent landmarks that remain in the same place for a protracted period of time. Indeed, a map that depicted objects whose position varied regularly may well be misleading rather than helpful. O'Keefe and Nadel (1978) picked up on this point and suggested that a cognitive map will not include cues that move from trial to trial. If spatial learning depends upon the formation of a cognitive map, then it follows from this proposal that animals will be unable to navigate with reference to a moving landmark. Biegler and Morris (1993, p. 633) succinctly captured this idea with the rule for spatial learning: "If it moves, don't use it as a landmark." The next experiment was conducted in order to determine whether animals make use of this rule when they must find a hidden goal.

The top left-hand panel of Figure 2 shows a similar pool to that used for the previous experiment, with the curtains drawn open so that the cues provided by the room are visible from within the pool. On this occasion, however, the submerged platform is at a fixed distance (30 cm) and a fixed direction (south) of a landmark on the surface of the pool. In an experiment based on this apparatus, Roberts and Pearce (1998) trained a moving landmark group with the landmark and the platform located in the same place for the four trials of every session, but these objects were moved, as one, to a different position at the start of each session. The figure thus shows, for the moving landmark group, two of the possible arrangements of the landmark and platform that would have been used in Sessions 1 and 2 of Stage 1 of the experiment. To find the platform accurately on the first trial of every session, it was therefore necessary to locate the landmark and then head in a certain direction, and for a certain distance, with reference to it. A stable landmark group was trained in the same way as the moving landmark group, except that the two objects remained in the same place within the

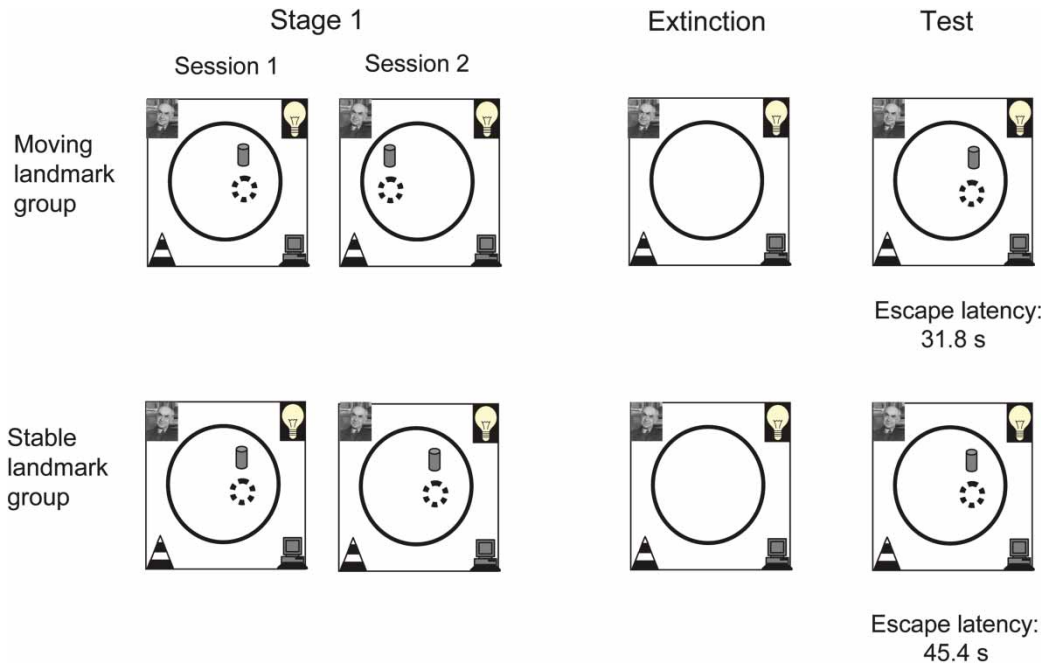


Figure 2. A plan of the apparatus used by Roberts and Pearce (1998) to study whether rats can use a moving landmark to locate a hidden goal. During Stage 1, the landmark was always 30 cm due north of the submerged platform. The symbols depict the same objects as those for Figure 1. To view a colour version of this figure, please see the online issue of the Journal.

pool throughout training. If landmark stability is an important prerequisite for spatial learning, then the stable landmark group will learn accurately about the position of the platform relative to the landmark within the pool. In contrast, the movement of the landmark within the pool for the moving landmark group will lead to it being disregarded as a cue for finding the platform. It is possible that this group might form a map swiftly in each session based on the stable room cues, but this map would be of no use for finding the platform on the first trial of each session. At first, both groups found it rather difficult to locate the platform, but as training progressed they became progressively more efficient at heading towards the platform after being released into the pool. Not surprisingly, this task was somewhat easier for the stable than the moving landmark group, particularly on the first trial of each session.

The main question of interest in this experiment was whether the moving landmark group

learned anything about the position of the landmark with reference to the moving landmark. To answer this question, rats next received extinction trials in which they were placed in the pool in the absence of the platform and landmark, but in the presence of the room cues. These trials were intended to reduce any control acquired by the room cues over searching for the platform. Finally a test trial was conducted in which the landmark and platform were returned to their original locations for the stable landmark group and to a similar location for the moving landmark group. The results displayed in the right-hand panel of Figure 2 show that it took the stable landmark group longer than the moving landmark group to find the platform. Furthermore, during the 60-s test trial, 7 out of 12 rats failed to find the platform in the stable landmark group, whereas only 1 out of 12 in the moving landmark group failed to find the platform.

These results are opposite to that expected if a landmark must remain in the same location in

order to participate in spatial learning. At the same time, the results are entirely in keeping with associative learning theory. According to this point of view, the only cue that can be used to find the platform reliably in the moving landmark group is the moving landmark, and it will thus gain full control over searching for this goal. For the stable landmark group, the landmark in the pool was no better than the landmarks outside the pool as a cue for finding the platform. Associative learning theory (e.g., Rescorla & Wagner, 1972) predicts that the landmark in this condition will be overshadowed by the room cues and gain less control over searching for the platform than in the moving landmark group.

A possible criticism of this experiment is that the moving landmark group did not learn that the platform was at a certain distance and direction from the landmark. As an alternative, this group might have learned to do nothing more than search in the vicinity of the landmark for the platform. Additional findings by Roberts and Pearce (1998) indicate that this criticism is unjustified. We trained a group in the same way as the moving landmark group, before presenting a test trial in which rats were placed in the pool with the landmark but not platform. During this test searching for the platform was concentrated in a region that was the correct distance and direction from the landmark.

Environmental shape and cue competition

The above experiments demonstrate that considerations, which will no doubt lead to the creation of a first-class map for human navigation, do not lead to findings that show there is a difference between spatial and associative learning. But it is not just the need to construct an accurate map that has led researchers to claim that spatial and associative learning are governed by different principles. Both Cheng (1986) and Gallistel (1990) have argued that certain aspects of spatial learning will be immune to the cue competition effects predicted by associative learning theory, even though their justification for this claim makes no reference to a cognitive map. They suggested that when animals

explore a new environment, they will construct a representation of its overall shape, which can then be used for finding hidden goals. They further argued that learning about the shape of the environment takes place in a dedicated "geometric module" that is impervious to nongeometric information. A theoretical justification for this claim concerning the impenetrability of the module is that animals must navigate through the same environment in different seasons. Although the objects that provide information about the shape of the environment remain constant, their physical characteristics may change, for example, by being covered in snow or by losing leaves. Navigation is thus likely to be more accurate when emphasis is placed on the geometric relations among objects, and rather little heed is paid to the details of their attributes (see Gallistel, 1990, p. 208).

An empirical justification for the dedicated nature of the geometric module was based on a study by Cheng (1986). Rats were trained to find food that was consistently located in one corner of a rectangular arena. One of the long walls of the arena was white, the remaining walls were black, and there was a distinctive landmark in each corner. If the apparatus had been composed of four white walls and contained no landmarks, then the shape of the arena would provide the only cue for finding food, and it would be impossible to distinguish the corner with food from the diagonally opposite corner. The addition of the landmarks and the white wall was intended to remove this ambiguity. Even so, it became apparent as training progressed that rats to some extent ignored the featural cues and relied on the shape of the environment to find the food. For example, most of the errors that were made during training consisted of heading to the corner diagonally opposite to where food was hidden. The fact that animals made use of information about the shape of the arena, when they did not need to, led Cheng (1986) and Gallistel (1990) to argue that learning about the shape of the environment takes place in a geometric module that excludes nongeometric information.

From the point of view of the present discussion, this conclusion is important because it

implies that effects such as blocking and overshadowing will not be observed between geometric and nongeometric cues. Cheng's (1986) experiment does not provide unequivocal support for this conclusion. It is possible, for example, that the presence of the landmarks and the single white wall restricted but did not prevent learning about the position of food with reference to the rectangular arena. The absence of an appropriate control group in this study makes it impossible to say whether such overshadowing took place. In view of this shortcoming, the next experiment was conducted in order to examine further the proposal that cue competition effects will not be found when a goal can be located by reference to geometric and nongeometric cues (Pearce, Graham, Good, Jones, & McGregor, 2006).

Two of the four groups in the experiment were trained to find a platform in a rectangular pool. The four walls were white (W) for the rectangle-W group, whereas for the rectangle-BW group one pair of short and long walls was black (B), and the other pair was white (see Figure 3). The rectangle was surrounded by curtains, and its orientation varied from trial to trial in order to ensure that only cues provided by the rectangle could be used to find the platform. After a number of sessions of training, rats in the rectangle-BW group on being released into the pool would head directly for the platform. Rats in the rectangle-W group would make a similar response, or else they would head directly for the opposite corner where they would search unsuccessfully for the platform before heading for the correct corner. This action is readily explained because the two corners visited by this group were geometrically identical and hence impossible to tell apart.

Upon the completion of this training, both groups received a single 60-s test trial in a rectangular pool constructed from four white walls, with the platform removed. The amount of time spent in 30-cm diameter search zones in the two geometrically correct corners, and the two geometrically incorrect corners, was then calculated. A correct corner was defined as one with the same geometric properties as the corner where the platform had been located originally. The total of

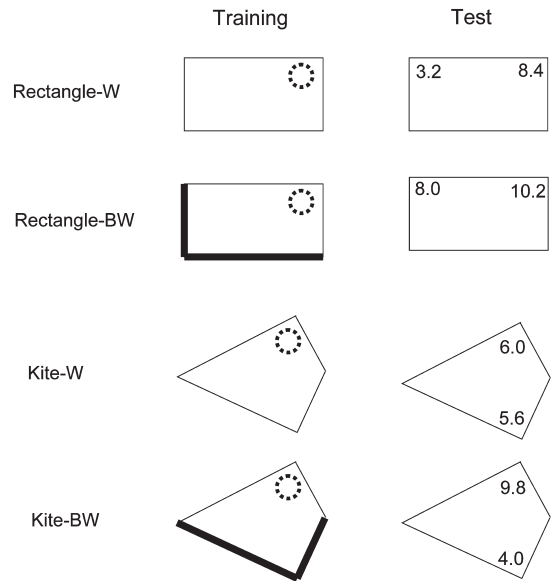


Figure 3. A plan of the apparatus used by Pearce et al. (2006) to study the influence of the colour of the walls on spatial learning based on the shape of the environment. Thin black lines depict white walls; thick black lines depict black walls. The numbers in the rectangles represent the percentages of time spent in search zones in the correct corners (top right corner) and the incorrect corners (top left corner), during a test trial without the platform. The numbers in the kite represent the percentages of time spent in the correct (upper corner) and incorrect (lower corner) right-angled corners during a test trial.

the time spent in the two geometrically correct corners is displayed, for each group, in the top right-hand corner of the appropriate rectangle in the right-hand column of Figure 3, and the total of the time spent in the incorrect corners is displayed in the other top corner. It is evident that the discrimination between the correct and incorrect corners was considerably greater for the rectangle-W than the rectangle-BW group.

The implication of these findings is that the presence of the black walls during the training stage disrupted learning about the significance of the shape of the rectangle for the rectangle-BW group. Of course, this result should not have been found if Gallistel (1990) was correct in asserting that the geometric module is impervious to nongeometric information. It follows directly from this proposal that the colour of the walls

will exert no influence over learning about the position of the platform with reference to the shape of the pool. At the same time, the results can be readily explained by associative learning theory. During the training stage, the platform could be found by referring either to the colour of the walls or to the shape of the pool. The two types of cue would then be in competition with each other, and the geometric cues would gain less control over searching for the platform than in the rectangle-W group.

The remaining two groups were trained and tested in the same way as the two groups just described, except that the apparatus was in the shape of a kite rather than a rectangle (see lower half of Figure 3). On this occasion, the test trial revealed that the group trained with four white walls, the kite-W group, performed rather poorly on the test trial, whereas the kite-BW group, which was trained with two black and two white walls, showed an excellent discrimination between the correct and incorrect corners of the white kite on the test trial. Once again, this outcome would not be expected if the colour of the walls of the arena is denied access to the geometric module. It must also be admitted that the results do not fit comfortably with an associative analysis as it has been presented thus far, because the coloured walls in the kite-BW group would be expected to overshadow, rather than potentiate learning based on the shape of the kite. As will be shown shortly, however, it is possible to provide, and test, an associative explanation for the results from the kite-BW and the kite-W groups.

A way of reconciling the present results with the suggestion that spatial learning based on the shape of the environment will be unaffected by the presence of nongeometric information is to point to the nature of the nongeometric cue that we used. It is conceivable that because colour was an attribute of the objects creating the shape of the environment it was allowed into the geometric module, where it then influenced learning about the shape of the environment in the manner predicted by associative learning theory. That is, only information about the objects creating the shape of the environment might be permitted

access to the module but, once in the module, the different attributes of the object may have to compete for associative strength according to well-established associative principles. Although this proposal is no longer in keeping with the detail of the proposals of Cheng (1986) and Gallistel (1990), it does not appear to violate too seriously their spirit. An implication of this brief discussion is that while the colour of the walls might influence learning based on the shape they create, the placement of landmarks in an environment with a distinctive shape will not have the same effect. More specifically, the landmarks would certainly not be expected to influence, or be influenced by, learning based on the shape of the environment (see also Doeller & Burgess, 2008).

The results from a number of experiments are relevant to the foregoing conclusion as the following unpublished experiment conducted with Murray Horne and Guillermo Esber demonstrates (see also McGregor, Horne, Esber, & Pearce, *in press*). The apparatus consisted of a triangular-shaped arena, created within a circular pool, with a submerged platform located in one corner at the base (see Figure 4). An overshadowing group was trained with a platform located always in the same corner and always with a ball suspended from the ceiling 30 cm directly above the platform (see upper panel of left-hand column of Figure 4). According to current theories of learning, the presence of the ball will restrict the control acquired by the shape of the pool for finding the platform. Likewise, the shape of the pool will overshadow learning about the significance of the ball for finding the platform. The first of these predictions was tested with a shape control group, which was trained with two balls suspended in the two corners at the base of the triangle (see middle panel of left-hand column of Figure 4). In order to discriminate between the two corners, it is essential for this group to attend to the shape of the pool, and theories of associative learning predict that the shape of the pool will gain more control over searching for the platform in this group than in the overshadowing group. To test this prediction, the two groups received a 60-s

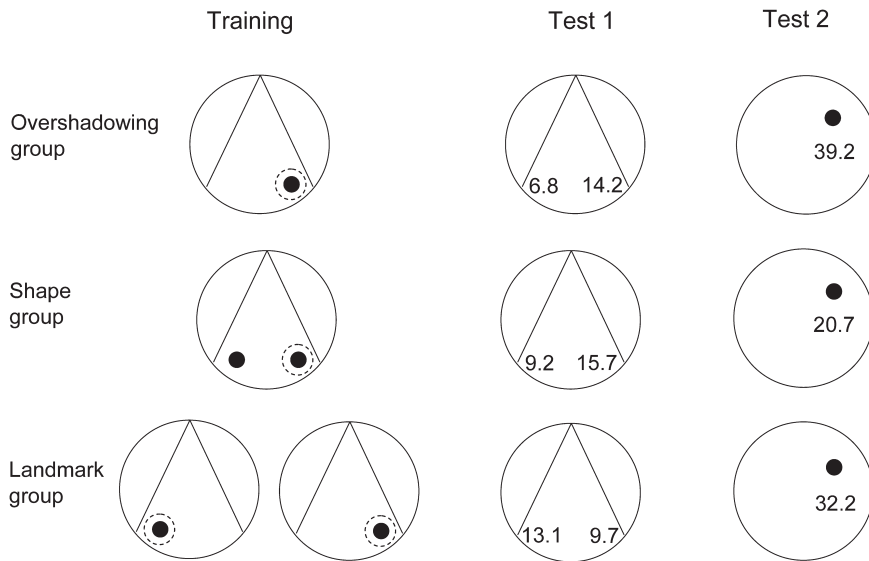


Figure 4. A plan of the apparatus for an unpublished experiment by Horne, Esber, and Pearce that failed to reveal overshadowing between spatial cues. The large circle depicts a circular pool, with two boards lowered vertically into it to create a triangular arena with a curved base. The small dashed circle depicts the submerged platform, and the filled black circles depict spherical landmarks suspended above the pool. The numbers depict the percentages of time spent by the three groups in search zones located in the two corners at the base of the triangle during Test 1 and in a search zone located beneath the spherical landmark in a circular pool during Test 2. The platform was absent for both tests.

test trial in the triangular pool with the landmarks and platform removed. The percentage of time spent in two 30-cm diameter search zones in the correct corner (the one where the platform was located) and the incorrect corner (the other corner at the base of the triangle) was recorded for each subject. The results from the test for the two groups are displayed in the appropriate panels in the middle column of Figure 4. Both groups showed a marked discrimination between the correct and incorrect corners, and there was no hint that the extent of this discrimination was greater in the shape than in the overshadowing group.

One factor that is known to influence overshadowing is the relative salience of the two stimuli: Overshadowing is more likely to be found if the stimulus to be overshadowed is weaker than the overshadowing stimulus than if the opposite is true (e.g., Mackintosh, 1976). Perhaps, therefore, the failure to detect overshadowing in the overshadowing group was due to the salience of the landmark being substantially less than that of the

geometric cues. If this is correct then it would follow that the geometric cues during the training stage would overshadow learning about the spherical landmark. This prediction was tested with a third group, which was trained with a single sphere always above the platform. Sometimes these objects were in one corner at the base of the triangle and sometimes in the other corner in order to ensure that the landmark gained the maximum possible associative strength. To compare the effectiveness of the training with the landmark in the three groups, the experiment concluded with a test trial in which the ball was suspended above the water, in the absence of the platform, in a circular pool. For the sake of consistency, the landmark group received the same test trial in the triangle as did the other two groups, but the results were of little interest because the group was not expected to express a preference for one corner over the other.

The mean percentage of time spent by the three groups searching in a 30-cm diameter circular search zone immediately beneath the landmark

during the 60-s test trial in the circular pool can be seen in the right-hand column of Figure 4. The training with the landmark group was clearly effective because this group spent a substantial proportion of the test trial beneath the suspended spherical landmark. When this result is compared with the result for the overshadowing group then it is evident that overshadowing did not occur in this experiment. Quite the opposite, the overshadowing group spent more time beneath the landmark than did the control group. Finally, the relatively small amount of time spent beneath the landmark in the shape group can be understood because the landmark was a less reliable predictor of where the platform could be found during the training stage than in the other two groups.

There is, therefore, no hint in this experiment of overshadowing between the landmark and the geometric cues. Such an outcome is consistent with the proposal that learning about geometric cues progresses independently of learning about individual landmarks (e.g., Cheng, 1986; Gallistel, 1990), but it is not consistent with the proposal that learning about these cues is governed by the same error-correction rule that is believed to dictate the course of associative learning (e.g., Rescorla & Wagner, 1972). Additional reports of a landmark failing to disrupt learning based on the shape of the environment, through either blocking or overshadowing, can be found in Hayward, Good, and Pearce (2004); Hayward, McGregor, Good, and Pearce (2003); Kelly, Spetch, and Heth (1998); Pearce, Ward-Robinson, Good, Fussell, and Aydin (2001); and Wall, Botly, Black, and Shettleworth (2004).

Miller and Shettleworth (2007) have argued that these failures of a landmark to restrict learning about the shape of the environment do not pose a serious challenge to an associative analysis of spatial learning. Indeed, they have developed a revised version of the Rescorla–Wagner (Rescorla & Wagner, 1972) theory and have shown how it can explain many of the published failures to observe overshadowing and blocking between individual landmarks and geometric cues provided by the shape of the environment. There is insufficient space to present a detailed

evaluation of this ingenious model here, suffice to say that McGregor et al. (in press) have argued that the model is unable to explain the results from Test 2 shown in Figure 4.

Between-cue associations and potentiation of spatial learning

One of the foregoing findings that merits further attention comes from the experiment whose design is summarized in Figure 3 (Pearce et al., 2006; see also Graham, Good, McGregor, & Pearce, 2006). In that experiment we found during a test trial in an entirely white kite that the kite-BW group was able to discriminate more accurately between the correct and incorrect corners than the kite-W group. The implication of this finding is that the presence of black and white walls for the training with the kite-BW group potentiated learning about the position of the platform relative to the geometric cues.

To understand how potentiation of spatial learning based on geometric cues might be explained, it is helpful to refer to the formation of between-cue associations (e.g., Rescorla & Durlach, 1981). During the initial training in the kite, the kite-BW group might learn to approach the geometric cues created by the correct corner and to avoid those created by the incorrect corner; the group might also learn to approach white and to avoid black. Associations might also develop between the geometric cues and the colour of the walls creating them. The sight of the incorrect geometric cues during the test in the white kite would then activate a memory of the aversive black walls and encourage the kite-BW group to swim away from this corner and towards the correct corner. Likewise, the sight of the correct geometric cues might activate a memory of the attractive white walls and act as a further inducement for this group to approach the correct corner. In the control group, the correct and incorrect geometric cues would be associated with the same cue—white walls—and lead to the choice on the test trial being determined solely by the associative strengths of the two geometric cues. As a consequence, the

preference for the correct over the incorrect corner in this group would be weaker than that in the experimental group.

To test the foregoing explanation Horne and Pearce (2008) gave two groups the training summarized in Figure 5. They were both first required to find a submerged platform in the black corner of a black and white kite. The two groups then proceeded directly to a revaluation phase in a square pool with one corner created from two black walls and the opposite corner created from two white walls. The platform was placed in the black corner for the consistent group and in the white corner for the inconsistent group. This treatment was intended to maintain the tendency of the consistent group to approach black and to avoid white and to reverse this tendency in the inconsistent group. Finally, both groups received two test trials, one in a kite with four black walls and one in a kite with four white walls, in order to assess the control of the geometric cues over searching for the platform.

The group mean percentages of time spent in search zones in the two right-angled corners of the kite are shown for the two groups for the two test trials in the right-hand half of Figure 5. The most important results are those from the

test trial in the white kite by the inconsistent group, which revealed that significantly more time was spent in corner W than in corner B. Thus the revaluation treatment in Stage 2 resulted in the inconsistent group preferring the corner with the geometric properties associated with the absence of the platform in Stage 1. The explanation for this outcome is that during Stage 1 rats associated corner B with black and corner W with white. In Stage 2 they then learned to avoid black and to approach white. As a consequence, in Stage 3, the sight of corner B would excite the memory of black, which, because of the training in Stage 2, should discourage approach to corner B. Of course corner W would activate a memory of white, which, because of the training in Stage 2, would encourage approach to corner W. The combination of these tendencies would then explain the preference for corner W over corner B. Given this analysis, the results from the test with the consistent group in the black kite are readily understood. The sight of corner W will evoke a memory of white, and because rats were trained to avoid white in Stages 1 and 2, the evoked memory of this colour in Stage 3 will encourage them to swim away from W and towards B.

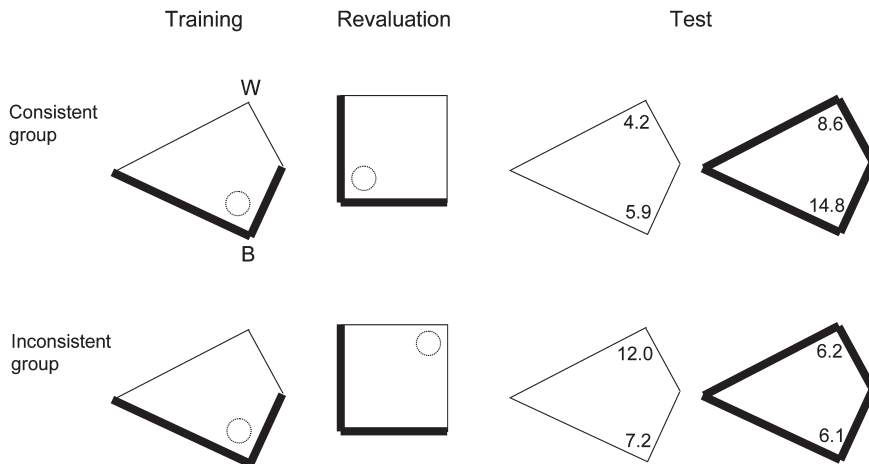


Figure 5. A plan of the apparatus used for an experiment by Horne and Pearce (2008) to study the influence of between-cue associations in spatial learning. Thin lines depict white walls of the arenas, thick lines depict black walls, and the dotted circle depicts the submerged platform. The numbers in the corners of the arena represent the percentage of time spent in the respective corners during a test trial with the platform removed.

The remaining findings from the test trials may seem more puzzling because rats spent similar amounts of time in corners W and B. Although this outcome is at odds with the explanation just put forward, it can be understood once it is appreciated that four walls of the test pool on these trials were the same colour as the corner that rats were trained to avoid in Stage 2. The implication of these two test trials is that rats are reluctant to head towards any corner with a colour they have recently learned to avoid.

During their training in a spatial task, therefore, rats do not just learn about the significance of individual cues, they also learn about the relationships between cues, and these relationships can exert a powerful influence on where they choose to head when seeking a hidden goal. Thus between-cue associations can lead to spatial learning being more flexible, and adaptable, than would be possible if it depends upon associations based solely on reinforcement.

The conclusion that between-cue associations develop during the course of spatial learning may help to explain other findings that at first sight appear to contradict predictions from associative learning theory. In particular, they might account for the repeated failures to demonstrate overshadowing and blocking between landmarks and geometric cues. For instance, if a platform is located beneath a landmark in one corner of a triangular pool, then the presence of one cue might overshadow the other. However, the two cues might become associated so that any detrimental effect of overshadowing will be compensated for by potentiation based on the between-cue association.

In support of this explanation, it is worth noting that several of our previous attempts to demonstrate overshadowing and blocking between landmarks and geometric cues have revealed a hint of potentiation (Hayward et al., 2004; Hayward et al., 2003; Pearce et al., 2001). There was even a hint of potentiation in the results shown in Figure 4, where a test trial in the circular pool resulted in the overshadowing group spending more time beneath the sphere than the control group. These demonstrations of potentiation have been frustrating because of

their elusiveness. They have been only occasionally statistically significant, and they are thus not easy to replicate. It is quite easy to understand why potentiation has proved hard to pin down, because it depends upon the influence of between-cue associations more than compensating for any disruptive effects of blocking, or overshadowing. There is no reason why potentiation should necessarily overcome the effects of cue competition. Instead, all that can be said with certainty is that the influence of associations between landmarks and geometric cues will make it difficult to reveal overshadowing and blocking with them.

One issue that remains is to identify the factors that determine when between-cue associations will be effective. It appears to be easier for a landmark within an arena to overshadow or block cues outside the test arena than to overshadow or block cues provided by the shape of the arena. This comparison might then be taken as an indication that between-cue associations form more readily with cues that are close together—landmarks and geometric cues—than cues that are far apart—landmarks within an arena and those outside it. However, a particularly strong demonstration of potentiation has been reported by Hayward et al. (2003, Experiment 3) using cues that were not close together. For the present, therefore, it is safest to conclude that spatial behaviour is influenced by between-cue associations, but the factors that determine when these associations will be maximally effective remain to be determined. It should also be emphasized that, at present, between-cue associations provide a possible explanation for the failures to find blocking and overshadowing with landmarks and geometric cues. There is, to my knowledge, no evidence that shows unequivocally that competition has occurred between these different types of cue and that it has been masked by the influence of associations between them. This point is pursued further in the “Concluding comments” section.

The nature of the geometric cue

For an associative explanation of behaviour to be complete it must specify the nature of the

components that enter into associations. This specification is relatively easy in the case of Pavlovian conditioning where the stimuli are quite simple—but it is more difficult in the analysis of spatial learning where the stimuli are relatively complex and where the animal has a large say in when it is exposed to them, and to what degree. Even so, the previous discussion placed considerable emphasis on the role that geometric cues play in spatial learning, and something needs to be said about how they are represented by an animal.

When Cheng (1986) first demonstrated that rats can refer to the shape of their environment in order to find a hidden goal, he argued that the position of the goal was defined with reference to the overall shape of the test apparatus. Thus, for Cheng (1986), the geometric cue was regarded as being a global representation of the environment. This proposal served as a powerful stimulus for research into spatial learning and resulted in investigations into how species ranging from goldfish to humans navigate with reference to an environment with a distinctive shape. By and large the results were consistent with those reported by Cheng (1986), and they were interpreted as showing that animals form global representations of the overall shape of their environment (Gouteux, Thinus-Blanc, & Vauclair, 2001; Hermer & Spelke, 1994; Kelly, Spetch, & Heth, 1998; Sovrano, Bisazza, & Vallortigara, 2002; Vallortigara, Zanforlin, & Pasti, 1990). See also Gallistel (1990).

Despite this influence of Cheng's (1986) proposals, his original experiment does not demonstrate unequivocally that animals identify the position of a goal with reference to the overall shape of the environment. The top left-hand panel of Figure 6 shows a rectangular arena with a submerged platform in one corner and with no additional cues to indicate the position of the goal. It is possible that during their training in this apparatus, rats acquired a representation of the overall shape of the pool and the position of the platform within it. Then, on being returned to the pool, they would be able to use this representation to determine where to search for the platform. This strategy is referred to as the

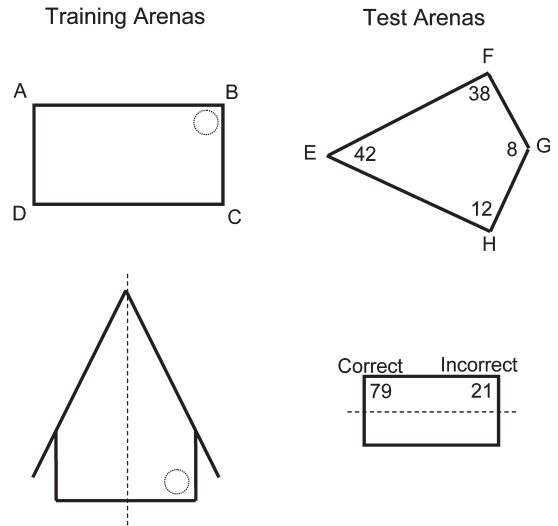


Figure 6. The shapes of the training and test arenas used by Pearce *et al.* (2004), top row, and by McGregor *et al.* (2006), bottom row, to study the transfer of spatial learning from one arena to another. The numbers represent the percentages of rats who headed directly for each corner in the kite, or the correct and incorrect corners in the rectangle.

global strategy because it is based on a global representation of the area. There are, however, two additional strategies that could be used in order to find the platform. Animals might look for the platform in a corner where a long wall is to the left of a short wall; or they might look for a wall of a certain length—say a long wall—and search in the corner at the right-hand end. These solutions are referred to, respectively, as the corner and wall strategy, and, because they are based on components of the overall shape, they can be said to depend upon a local representation of the arena. Each of the three strategies will lead to the rat searching in the corner with the platform and the diagonally opposite corner, and there is nothing in the results described by Cheng (1986), or in the experiments described in the references cited above, to indicate whether subjects rely on a global or a local strategy when seeking a goal in an environment with a distinctive shape.

In an attempt to identify which of the three strategies rats use, Pearce, Good, Jones, and McGregor (2004) first trained 20 rats to find the

submerged platform in the rectangular pool displayed in Figure 6. The orientation of the pool was varied randomly from trial to trial, and the pool was surrounded by curtains, in order to ensure that the only cues available for finding the platform were provided by the shape of the apparatus. After 11 sessions of training, the rats were transferred to the kite-shaped arena shown in the upper right-hand panel of Figure 6, and a record was taken of which corner they headed to first. The kite was constructed from the same walls as the rectangle, and corners F and H were both right-angled. Thus corner F is geometrically equivalent to the corner housing the platform in the rectangle, corner B.

If the platform was found in the rectangle by reference to a global representation of its overall shape then, on being placed in the kite, the rats should effectively be lost. The lack of correspondence between the shapes of a kite and a rectangle will mean that a global representation of a rectangle will be of no value in the kite, and the rats should fail to express a preference for one corner over another. On the other hand, if rats were to adopt one of the local strategies in the rectangle, then they should behave in a predictable manner in the kite. The adoption of the corner strategy in the rectangle, for example, will lead them to search predominantly in Corner F in the kite. The effect of adopting the wall strategy will be determined by which long wall in the kite the rat selects after being released. If it should select EF then swimming to its right-hand end will lead it to corner F, but if it should select EH then the same response would lead to the apex of the pool. The numbers in the four corners of the kite in Figure 6 depict the percentage of rats that headed directly for each corner after being released into the pool for the test trial. There was a strong tendency for the group to head either for E, the apex of the pool, or corner F. Relatively few rats headed directly for the remaining two corners. This pattern of results is just what would be predicted if the platform was found by the long wall strategy in Stage 1 and if the same strategy was adopted when the group was released into the kite. The preference for Corner F over corner H

can be explained by the use of the individual corner strategy in both environments, but some reason is then needed to explain why rats showed such a strong tendency to search in the apex. Finally, the fact that some corners were preferred over others poses a challenge to the suggestion that rat navigated with reference to a global representation of the overall shape of the pool in the first stage of the experiment. In view of this challenge, and given that the results are entirely consistent with the suggestion that rats adopted the wall strategy to find the platform, Pearce et al. (2004) concluded that navigation in environments with a distinctive shape is controlled by local rather than global cues.

It was not long before this conclusion was challenged. Cheng and Gallistel (2005) suggested that rather than construct a global representation based on the entire shape of the arena, as Cheng (1986) originally proposed, animals might represent their environment in more abstract terms based on its principal axis (see Gallistel, 1990). The principal axis of the rectangle is the line that divides it in half along its length, and the principal axis of the kite is the line that joins corners E and G. During their training in the rectangle, Cheng and Gallistel (2005) proposed that rats might learn to search as far as possible to the left at one end of the principal axis. They further proposed that if this strategy were to transfer to the kite then it would result in rats searching in either corner E or corner F.

McGregor, Jones, Good, and Pearce (2006) tested this explanation by training rats to find a submerged platform in the corner of the house-shaped arena shown in the lower, left-hand corner of Figure 6, before they were tested in the rectangle shown in the lower-right hand corner. The walls of the rectangle were of the same length as the walls of the rectangle that forms the base of the house. If rats navigate with reference to local cues, then they would be expected to search in the two corners that were geometrically equivalent to the correct corner in the house—the correct corners. These corners could be found by swimming either to a corner with certain geometric properties, or to the left-hand

end of a wall that is of the same length as the wall at the base of the house. Thus if rats were to adopt either a corner or a wall strategy in the training arena, they should head toward a correct corner in the test arena. On the other hand, if rats find the platform by referring to the principal axis of their environment, then the opposite outcome is predicted. The dashed lines in both figures depict their principal axes. To find the platform in the training arena, rats would have to search far to the left at the end of the principal axis. The transfer of this strategy would then take them to the incorrect rather than correct corners in the rectangle. The numbers in the two corners in the rectangle in Figure 6 represent the percentages of rats that headed directly for the two correct corners and the two incorrect corners of the rectangle during the test trial. It is evident that considerably more animals swam straight to a correct than an incorrect corner, which again suggests that rats do not navigate by reference to global cues in an environment with a distinctive shape.

The possibility remains that rats navigate by means of both global and local cues, but they preferred to rely on the latter during the test trials that have just been described. It is not easy, however, to think of an experiment that would test this possibility, and, guided by the principle of parsimony, the most reasonable conclusion to draw is that animals navigate with reference to local rather than global cues in environments with a distinctive shape. In support of this conclusion, it is noteworthy that when discussing whether animals make use of cognitive maps, others have also concluded that animals do not navigate with reference to the global properties of their environment (e.g., Benhamou, 1996; Bennett, 1996; Healy, Hodgson, & Braithwaite, 2003; Mackintosh, 2002; Pearce, 2008).

The neural basis of spatial learning

The different techniques that have been described in this article were developed in order to enhance our understanding about the conditions that promote spatial learning and to identify some of

the information that is acquired during a spatial-learning task. The final topic to consider is whether the findings from these and related techniques can also enhance our understanding of the neural basis of spatial learning.

There is no doubt that one region of the brain that plays an important role in spatial behaviour is the hippocampus. Morris, Garrud, Rawlins, and O'Keefe (1982), for example, have shown that hippocampal lesions markedly impair the ability of rats to find a submerged platform in a circular pool by reference to landmarks outside the pool. The issue that remains is to specify the function of the hippocampus in spatial learning, and the following experiments were conducted with this aim in mind.

The first experiment was based on the design shown in the left-hand panel of Figure 2 (Pearce, Roberts, & Good, 1998). A control group of rats and a group with hippocampal lesions were required to find a platform that was 20 cm in a fixed direction from a landmark in a circular pool surrounded by cues provided by the experimental room. It is important to stress that the landmark and platform remained in the same place for the four trials of each session, but they were moved as one from session to session. During the majority of the 11 training sessions, the hippocampal group found the escape platform more swiftly than the control group on the first trial of each sessions, whereas the control group found the platform more swiftly than the hippocampal group on the fourth and final trial of each session (see Figure 7).

To explain these results, we argued that the platform could be found by means of two different strategies in the control group. They could find it either by referring to the landmark within the pool—the local landmark strategy—or by reference to its position to the landmarks outside the pool—the distant landmark strategy. We further argued that the distant landmark strategy, but not the local landmark strategy, was disrupted by hippocampal lesions. Thus for the first trial of a session, the control group would be torn between adopting the local landmark strategy, which would lead it to the correct location, and the

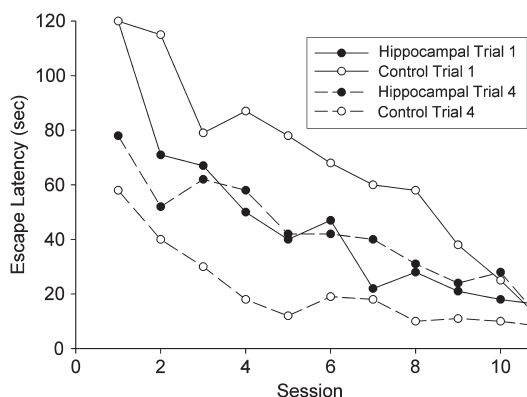


Figure 7. *The mean escape latencies for a group of rats with hippocampal lesions, and a sham operated control group, that were required to find a submerged platform 20 cm in a fixed direction from a landmark located in a circular pool. The landmark and platform remained in the same place for the four trials of a session, but were moved as one to a new position each session. The results are shown for the first and fourth trials of every session.*

distant landmark strategy, which would lead it to where the platform was located on the previous session. In contrast, by having to rely on just the local landmark strategy, the hippocampal group would head directly for the platform and presumably take less time to find it than the control group. By the time of the fourth trial, however, the control group would have had time to learn about the new position of the platform with reference to the distant landmarks. The combined influence of both strategies would then enable the control group to reach the platform more swiftly than the hippocampal group, which would again be forced to rely on a single strategy. The implication of these findings, therefore, is that rats can use at least two different strategies to find a hidden goal that is some distance from one or more landmarks, and that these strategies are governed by different regions of the brain.

The findings from the foregoing hippocampal study correspond remarkably well with the results from an elegant study by Doeller et al. (2008), using functional magnetic resonance imaging (MRI) with humans. In a task that was very similar to the one used by Pearce et al.

(1998), participants were asked to find a hidden object in a virtual environment with a boundary, distant landmarks beyond the boundary, and discrete landmarks within the boundary. Participants on some trials were required to use the local landmark strategy to find an object, on which occasion there was activity in the right dorsal striatum, and on other trials they were required to make use of the distant landmark strategy, or as Doeller et al. (2008) refer to it, the boundary strategy, when there was activity in the hippocampus. It thus appears that for both rats and humans the hippocampus plays a prominent role in the distant landmark strategy. It also appears that for both species a different brain region is involved in the local landmark strategy. This is not to say, however, that the two strategies operate entirely independently. It was mentioned earlier that when Roberts and Pearce (1998) conducted an experiment based on the design just described, we found that if the platform and landmark remained in the same place throughout the experiment, then the distant landmark strategy overshadowed the local landmark strategy. A similar outcome has been reported with humans by Doeller and Burgess (2008).

There is therefore strong evidence for the involvement of the hippocampus in spatial learning, and to at least some extent this involvement is the same for rats and humans. In order to gain a more detailed understanding of the role of the hippocampus in spatial learning, a series of experiments was conducted in which rats with hippocampal lesions and control rats were trained to find a submerged platform in the different environments shown in Figure 8 (Jones, Pearce, Davies, Good, & McGregor, 2007; McGregor, Hayward, Pearce, & Good, 2004; Pearce et al., 2004). In order to minimize the influence of distant cues, all of the arenas were surrounded by curtains, and their orientation was altered randomly from trial to trial.

The lesions did not have an influence on the ability of rats to locate the platform in the position shown in the two environments in the top row of Figure 8. In these environments the platform was located in the apex of a kite with four white walls

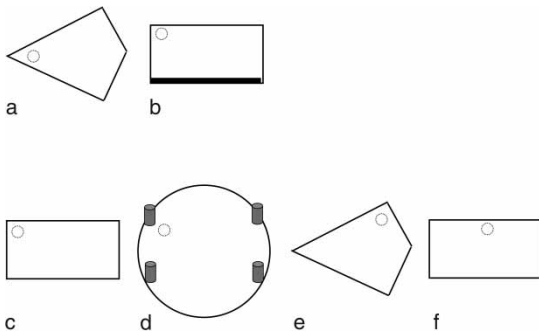


Figure 8. Plans of the arenas used by McGregor et al. (2004) and by Jones et al. (2007) to investigate the effects of lesions to the hippocampus on spatial learning based on cues provided by the shape of the environment.

(Figure 8a), or in a white corner of a rectangle with three white walls and one long black wall (Figure 8b). The lesions did, however, disrupt performance in each of the environments shown in the bottom row. In these environments, the platform was located in one corner of a rectangle with four white walls (Figure 8c), in one corner of a rectangle created by four vertical cylinders attached to the wall of a circular pool (Figure 8d), in a right-angled corner of a kite built from four white walls (Figure 8e), and in the middle of a long wall of a rectangle built from four white walls (Figure 8f).

The platform in the top two environments, but not the bottom four, can be found by swimming in a particular direction with reference to a distinct feature—the acute corner in Figure 8a and the black wall in Figure 8b. Thus hippocampal lesions do not appear to disrupt the capacity to navigate with reference to a single cue. It has just been proposed that animals will find the platform in Figure 8c by swimming in a particular direction with reference to the long wall. The disruptive effect of hippocampal lesions in this task, therefore, points to the conclusion that rats were unable to tell the difference between the long and short walls. A similar inability would explain the disruptive effects of the lesions in the other arenas depicted in the bottom row of Figure 8, because rats would then find it difficult to discriminate between the correct and incorrect cylinders in

Figure 8d, between the correct and incorrect right-angled corners in Figure 8e, and between the middle of the long and short walls in Figure 8f.

Furthermore, if hippocampal lesions impair the ability to make judgements based on relative lengths, and distances, then it should not be surprising that they impair performance in a standard Morris pool when the platform must be located by its relative position to two or more distant landmarks. Without doubt, there are alternative explanations for these results, and there remains the matter of understanding why decisions concerning relative distance are impaired by hippocampal lesions. Nonetheless, we can hope that by developing the different procedures described here, it will be possible to gain a deeper appreciation of the role of the hippocampus, and other brain regions, in spatial learning.

Concluding comments

Two principal conclusions can be drawn from the experiments reviewed above. The first is that cue competition effects such as blocking and overshadowing can be found with spatial learning. The demonstration of these effects provides evidence of the widespread influence of the laws of associative learning. In particular, these results suggest that spatial learning is governed by an error-correction rule (e.g., Rescorla & Wagner, 1972), which results in the cue that is the most reliable predictor of the location of a goal gaining greatest control over behaviour.

One set of results that does not fit entirely comfortably with this conclusion comes from experiments that have examined whether a landmark can disrupt learning based on the shape of the environment. The majority of experiments have revealed a total absence of overshadowing and blocking in these circumstances, which lends support to the claim that the rules that govern learning about the shape of the environment (Cheng, 1986; Gallistel, 1990), or its boundaries (Doeller & Burgess, 2008), are different to those that govern learning about landmarks. It might be wise to keep an open mind about this claim. On the one hand, we have seen that learning

based on the shape of the environment can be disrupted by the presence of certain cues, such as the colour of the walls. We have also seen that associative learning theory can provide a plausible explanation for the failures to find overshadowing and blocking, in terms of between-cue associations. On the other hand, there is no unequivocal evidence that the failure to detect overshadowing and blocking is due to these effects being masked by associations between landmarks and geometric cues. The obvious implication of this discussion is that there remains a need for further experiments to evaluate whether there is something special about spatial learning based on boundaries, or the shape of the environment.

The second principal conclusion to be drawn is that animals navigate with reference to local rather than global cues provided by their environment. This conclusion was based on findings from experiments in arenas of distinctive shapes, but similar results have been obtained with shapes created by individual landmarks (Esber, McGregor, Good, Hayward, & Pearce, 2005). The implication of these findings is that animals do not rely on a global representation of their environment, such as a cognitive map. Instead, they appear to search for a hidden goal on the basis of its spatial relationship with local cues. It must be left to future research for the nature of these local cues to be specified precisely. For instance, the experiments described above failed to provide any evidence that animals rely on geometric information of the sort, "short wall to the left of the long wall", in order to identify where a goal is located. Whether they are ever able to use this sort of information remains to be determined.

Associative learning theory has made a profound contribution to our understanding of conditioned behaviour, and it should perhaps not be surprising to learn that it can be applied with considerable success to the spatial domain. Not only can this class of theory explain a variety of findings from investigations of spatial learning, but devising ways of testing an associative account of spatial learning has led to the development of useful new techniques. The application of associative principles to spatial learning has thus

enhanced our understanding of the knowledge that is acquired during a spatial task and of the conditions that promote its acquisition.

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