A Study of Spatial Learning Based Upon the Shape of an Environment

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Part I

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Acknowledgements

Some journeys in life are rather more straightforward than others. The completion of this thesis certainly falls into the latter category. Many difficulties have been put in my path along the way, not least a debilitating illness which has prevented my completing this work for a considerable amount of time. Some people thought I would never see the fruits of my labour and I was one of them. Even so, here it is: finished. There are many people I should like to thank for helping me. First I must thank Professor John Pearce not only because of the constructive and sometimes challenging comments he has made regarding my work but also for the tremendous amount of patience and leniency he has shown concerning its late submission. I should also like to thank Professor Mark Good who has also made many valuable contributions to my work and offered, when needed, a supportive ear as well the opportunity to exchange entertaining stories about the ups, downs and even the crashes involved in mountain biking (a very welcome diversion indeed!). There have been many people, academic and support staff alike, who have enabled the submission deadline for this work to be extended time and time again and earnestly I thank them all for all their efforts. My deepest and most heart felt thanks, however, is reserved for Dr Lisa Evans who has helped me when no-one else would in more ways I can begin to remember.

Publications

Many parts of this thesis have been published in the following journals:

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Hayward, A., J., Good, M., Pearce, J., M. (2004). Failure of a landmark to restrict spatial learning based on the shape of the environment. *The Quarterly Journal of Experimental Psychology, 57 (4), 289-314.* times cited: 2

Mcgregor, A., Hayward, A., J.,Good, M., Pearce, J., M.(2004). Hippocampal lesions disrupt navigation based on the shape of environment. *Behavioural Neuroscience 118 (5) 1011-1021.* times cited: 5

Hayward, A., J., McGregor, A., Good, M., Pearce, J., M. (2003). Absence of overshadowing and blocking between landmarks and the geometric cues provided by the shape of a test arena. *The Quarterly Journal of Experimental Psychology, 2003, 56B (1)*114-126. times cited: 20

Summary

In nine experiments rats were required to escape from a swimming pool of opaque water by swimming to a submerged platform. The position of the platform was determined by the shape of the pool, which was either rectangular or triangular. In Chapter 2, a spherical landmark, above the surface of the water, failed to overshadow (Experiment 1) and block (Experiments 2 & 3) learning about the position of the platform relative to these shapes. The same landmark also failed to overshadow learning to find the platform relative to a rectangle described by four identical landmarks (Experiment 4).

Experiments in Chapter 3 provided equivalent results with cues situated outside the pool (Experiments 5a & 5b). Experiment 6 revealed that the presence of the triangular-shaped pool potentiated learning based on the cues which surrounded it.

In Chapter 4, a landmark was attached to the platform which potentiated learning based on the rectangular pool (Experiment 7). The results of Experiment 8, however, make it unlikely that such potentiation resulted from associations developing between the shape of the pool and the landmark (Experiment 8).

These findings offer little support to theories of associative learning like the Rescorla-Wagner model (1972) but are in general agreement with the proposal that animals possess a dedicated Geometric Module, impenetrable to featural information (Cheng, 1986; Gallistel, 1990).

The results of Experiment 9 may bring this interpretation of the results into question. In that study, rats were trained to find a submerged platform in one corner of a rectangular, and then a kite-shaped pool. In the kite the platform was easier to find if it was located in a corner congruent with the corner it had previously occupied. Rats must have therefore found the platform with reference to local cues rather than the overall shape of the pool.

(Part I) Chapter 1.

1. 01. Cue Redundancy and Cue Competition

Navigation is the process that permits the identification of a course or path to be maintained from one place to another (Gallistel, 1990). It allows animals to find food, water, shelter, a suitable mate and to know not only the whereabouts of predators but also their territorial limits so that conflict with neighbouring animals might be avoided. All these activities are fundamental for survival.

As a result of the tremendous diversity found across the animal kingdom and of habitat variety it is perhaps not surprising to find that animals use a range of cues to navigate. Even so, the primary focus of the current thesis is the way animals use visual landmarks to traverse short distances. Of particular interest are the mechanisms that influence animals to select one out of what may be several suitable landmarks as a cue for navigation. In the natural environment the location of a desired goal such as food may be described by a single or several prominent landmarks situated nearby as well as elements of the surrounding topography like a neighbouring mountain or stream. Under conditions of redundancy like the one just described the critical question to ask is *"which cue or set of cues might an animal rely upon to search for a hidden goal?"* In general terms there have been at least two classes of answer to this question and each is summarised succinctly below.

Some authors (Chamizo, Sterio & Mackintosh, 1985; Redhead, Roberts Good & Pearce, 1997) have argued that in situations involving landmark redundancy the laws of associative learning that govern Pavlovian conditioning (Mackintosh, 1975; Pearce & Hall, 1980; Rescorla & Wagner, 1972) influence which landmark an animal will rely upon to search for a goal. A critical assumption of these theories is that cues compete with each other for the control they acquire over behaviour. Thus, if an animal selects one landmark to navigate towards a goal, the extent to which another landmark is used for this purpose may be restricted.

Alternatively, other authors have argued that spatial learning is fundamentally different from Pavlovian conditioning (O'Keefe & Nadel, 1978; Cheng, 1986; Gallistel, 1990). As such, under conditions of redundancy competition between landmarks should not be observed. An obvious strategy for choosing between these two conflicting points of view is to examine whether cue competition effects such as blocking and overshadowing can be found in spatial tasks. Before reviewing the relevant evidence, I shall first describe these effects and how they are explained by two prominent, yet divergent, theories of associative learning: that proposed by Rescorla and Wagner (1972) and that advocated by Pearce (1984; 1990; 2002).

1.02. Blocking and the Rescorla-Wagner Model

According to Kamin, blocking is observed when prior establishment, as a signal for reinforcement, of one element of a compound stimulus restricts or blocks the amount learned about the second element (Kamin, 1968; 1969). In one experiment with rats, Kamin (1969) gave an experimental group conditioning trials in which noise was paired with shock. Subsequently the experimental group and a control group received trials in which they received compound presentations of the noise and light followed by a shock of the same magnitude and duration as the original one. Test trials showed a stronger conditioned fear response in the presence of light for the control than for the experimental group. It thus appears that pre-training the experimental group with noise restricted or blocked learning about the significance of the light in the compound stage. To explain this outcome Kamin argued that subjects learned the noise accurately predicted shock in the first stage and this led to an unsurprising unconditioned stimulus (US) when rats received compound presentations of the noise and light during the final stage.

A more formal account of blocking than the one offered by Kamin (1969) is provided by the Rescorla-Wagner model (1972) which is summarised by the equation below:

$$\Delta V = \alpha . \beta \, (\lambda - \Sigma V)$$

Before dealing with blocking itself, it is perhaps important to consider some of the more fundamental assumptions of the model. First, repeatedly pairing the conditioned stimulus (CS) with unconditioned stimulus (US) should gradually increase the strength of the association that forms between them (V). The growth of that association ceases when the combined associative strength of all CSs present on any given trial (ΣV) is equal to the associative strength supported by the US (λ), which is finite. Second, the development of the CS-US association is not uniformly incremental across trials. Instead the change in associative strength (ΔV) is determined by the difference between the current level of associative strength acquired by the CS and the maximum possible that the US can support ($\lambda - \Sigma V$). Thus, at the outset of conditioning this difference will be large and the CS should acquire substantially more associative strength than at the end of conditioning when this difference is small. The parameters α and β represent the salience of the CS and US, respectively. During conditioning these parameters have a set value between 0 and 1 and the role α plays in conditioning shall be made clear later in the discussion of overshadowing.

Because the Rescorla-Wagner model (1972) further assumes that CSs are in competition with each other to enter into an association with the US, it offers a rather straightforward explanation of blocking. Reconsider the study conducted by Kamin (1969) in which conditioning was conducted with the noise prior to its being presented in compound with the light. According to the Rescorla–Wagner model as the associative strength of the pre-trained stimulus increases it will restrict the amount of associative strength acquired by any stimulus accompanying it during the second stage. It thus follows from the Rescorla-Wagner model that the noise must have acquired sufficient associative strength during pre-training to restrict that acquired by the light, ensuring that animals were unable to learn about the significance of this added stimulus in the compound stage.

1.03. Overshadowing and the Rescorla-Wagner Model

Overshadowing provides another demonstration of cue competition in Pavlovian conditioning. This term refers to the finding that when animals are conditioned with two stimuli in compound, at least one will gain less associative strength than if they were separately paired with same US (Kamin, 1969; Pavlov, 1927). The Rescorla-Wagner Model (1972) assumes that overshadowing is dependent on the relative salience (α) of the two stimuli. If the salience of each element present in a compound stimulus is equal they should acquire the same amount of associative strength. In these circumstances overshadowing is predicted to be reciprocal. Another possibility is that one stimulus will be more salient than the other and under these conditions the

Rescorla-Wagner model (1972) predicts that the former should acquire more associative strength than the latter.

1.04 Cue Competition and Configural Theory.

Blocking and Overshadowing can also be explained equally well by the configural theory of associative learning proposed by Pearce (1987; 1994; 2002). One important difference between the elemental approach of the Rescorla-Wagner model and the configural stance adopted by Pearce concerns the assumptions that are made about the associations that form when conditioning is undertaken with a compound comprising two or more CSs. According to the Rescorla-Wagner model (1972) each element of the compound will form separate associations with the US. By comparison Pearce describes a connectionist model in which events such as CSs become associated with the US via configural units. According to this point of view when a compound is presented an association will form between the US and the entire pattern of stimulation evoked by the compound, or configural unit. Thus when a compound AB is presented it will fully activate an AB configural unit, which will become associated with the US. Moreover, following conditioning with AB, presenting A will, at least partially, activate the AB configural unit and weak conditioned response (CR) will be elicited .

The strength of the association (V) that forms between the configural unit, AB, and the US is predicted to develop gradually over a number of trials and is given by the equation below:

$$\Delta V_{AB} = \beta (\lambda - V_{AB}).$$

An important aspect of Pearce's model is stimulus generalisation which is summarised below:

$$\mathbf{E_A = {}_{A}S_{AB} \cdot V_{AB}}$$

According to the equation above the conditioned response (CR) elicited by an animal on any given trial will depend on the level of activation of the AB configural unit multiplied by its current level of associative strength (V_{AB}). Thus, if AB is presented and training with it has reached asymptote, then the configural unit for AB will become fully activated and animals will elicit a strong CR. If however, either A or B are presented on their own then the activation of the AB configural will be considerably less than if AB had been presented and the CR will be weak. Hence, the strength of the CR when element A is presented (E_A) is determined by its similarity to the AB compound (${}_{A}S_{AB} \cdot V_{AB}$).

The value of ${}_{A}S_{AB}$ can derived by this final equation:

$$\mathbf{{}_{P1}S_{P2} = N_C/N_{P1} * N_C/P_2}$$

P1 and P2 refer to the two patterns of stimulation evoked by A and AB, whilst NC describes the number of input units common to the two patterns. The AB compound has one element in common with A which gives NC in the current example a value of 1. N_{P1} and N_{P2} refer to the input unit elements activated by the patterns A and AB: the latter pattern of having 2 and former having 1.

It should be clear from the above discussion that the configural theory described by Pearce (1987; 1994; 2002) can offer a simple explanation of overshadowing. According to Pearce, conditioning with an AB compound will result in an association forming between the AB configural unit and the US. Conditioned responding in the presence of A will therefore be relatively weak, because it will be unable to fully activate the configural unit for AB. Moreover, the CR elicited by A will be weaker than if animals had been conditioned with just A. For simplicity I have ignored the influence of stimulus salience and the parameter β. Even so, as with the Rescorla-Wagner model (1972), Pearce's configural theory correctly predicts that learning based on A will be restricted if it is presented in compound with another stimulus.

Slightly more complex is how the configural theory proposed by Pearce (1987; 1994; 2002), accounts for blocking. For clarity reference shall be made to the study conducted by Kamin (1969) mentioned earlier, and attention shall be drawn first to the control group. Assuming that conditioning with AB had reached asymptote, presenting B during a test trial would be expected to activate the AB configural unit to half its maximal value (or 0.5), and the CR elicited by B would be relatively weak. For the experimental group, pre-training with A will have ensured that the configural unit for A became associated with the US and after sufficient training the strength of this association will be equal to λ. Due to the process of stimulus generalisation presenting AB in the compound stage will have the result of activating the configural unit for A to half its maximum value, or 0.5, and the CR elicited by it will be weak. Training with the compound will also increase the associative strength of the configural unit for AB until it has reached 0.5λ. When B is presented on its own during the test trial, it will activate the configural for AB, but only to half of its maximum value and will result in a CR equal to 0.25λ. Thus, learning based on B will be blocked by pre-training with A.

It is evident from the above discussion of the Rescorla-Wagner model (1972) and the configural theory of Pearce (1987; 1994; 2002) that they provide an elegant theoretical account for the occurrence of competition between stimuli in Pavlovian conditioning. One logical extension of these theories is to apply them to situations involving landmark redundancy. As noted earlier many authors have done just that, especially regarding the Rescorla-Wagner model (see Chamizo et al, 1985; Redhead et al 1997). Applied in this way models of associative learning (Rescorla & Wagner; Pearce) can be used to predict that competition should arise when the position of a goal is described by more than one landmark. There are thus theoretical reasons to suppose that overshadowing and blocking should be found in spatial tasks. Spatial learning theories (O'Keefe & Nadel, 1978; Cheng, 1986; Gallistel, 1990), however, predict the complete absence of cue competition effects in spatial tasks and the following section is devoted to understanding why this should be the case.

1.05. The Cognitive Map Hypothesis

According to O'Keefe and Nadel (1978) animals have two learning systems that enable them to navigate effectively. The first one, the Locale System, utilises a Cognitive Map (Tolman, 1948; O'Keefe & Nadel, 1978; Gallistel, 1990) which is *"the representation of a group of places, some related to others by means of a set of rules of spatial transformation"* (O'Keefe & Nadel, 1978, p. 86) and *"a map-like representation which acts a framework for organising [an organisms] sensory inputs and is perceived as remaining stationary in spite of the movements of the organism"*

(O'Keefe & Nadel, 1978, p.488). The Cognitive Map permits animals to determine their position relative to a goal irrespective of their current location and contains information about the geometric relations among all the landmarks that occupy an environment. Such information shall be referred to as spatial knowledge.

One important feature of the Cognitive Map Hypothesis (O'Keefe & Nadel, 1978) is that the laws of associative learning do not govern the acquisition of spatial knowledge on the map. Instead spatial knowledge is acquired in an all-or-none manner. The map is continually and spontaneously updated and re-adjusted in response to changes in the environment and it is for this reason that landmarks do not compete for the control they acquire over searching. Hence, blocking and overshadowing should not be found in spatial tasks that employ the Locale System.

The other learning system postulated by O'Keefe and Nadel (1978) is the Taxon System. It is less flexible than the Locale System and can be used to approach a desired goal irrespective of its location. It is the Taxon System, for example, that allows animals to find a goal by heading directly towards a single prominent landmark rather than by a configuration of landmarks. And there is sufficient evidence to suggest that animals are capable of doing just that. Morris (1981) for example trained rats to escape from a circular pool, filled with opaque water, onto a black platform visible above the water's surface. Using similar apparatus, Redhead et al (1997) required rats to find a submerged platform with reference to a landmark attached to it that could be seen above the waterline. In each of these studies no other landmarks were present and for each trial the platform and the location from which rats were released into the pool varied. Despite these precautions, rats succeeded in escaping rapidly from the pool onto the platform. Unlike its counterpart the Taxon System is subject to the same laws that govern associative learning. Thus if a task utilises the Taxon System then competition between landmarks should occur.

1.06. The Geometric Module

Cheng (1986) and Gallistel (1990) also suggest that animals possess a Cognitive Map, or in their terms a Metric Frame. For them the Cognitive Map is "*a record in the central nervous system of the macroscopic geometric relations among surfaces in the environment used to plan movements through the environment* (Gallistel, 1990, p. 103). The implications of this definition shall be discussed in the final part of the thesis.

Unlike O'Keefe and Nadel's (1978) conceptualisation of the Cognitive Map, the Metric Frame does not encode the distances and angles between landmarks: instead it records the overall shape of the environment in terms of displacement properties (Cheng, 1986; Gallistel, 1990). As such an enclosed rectangular environment, which has axial symmetry, might be described as comprising two pairs of geometrically equivalent corners. One pair of corners has the short wall to the left of the long wall, whilst this arrangement is reversed for the other pair of corners. By using the Metric Frame animals can disambiguate one pair of geometrically equivalent corners from the other. There are, however, very few situations in their natural environments in which animals are presented with geometric ambiguity. Indeed it is normally only in the laboratory that researchers impose such conditions (Hayward, McGregor, Good & Pearce, 2003; McGregor, Hayward, Pearce, & Good, 2004; Esber, McGregor, Good, Hayward & Pearce, 2005).

Animals can also navigate with reference to landmarks and Cheng (1986) and Gallistel (1990) argue they do so by relying on a Featural Subsystem. This subsystem is not dissimilar to O'Keefe and Nadel's (1978) Taxon System, with the exception that landmarks or features are not approached unless they appear in the correct place on the Metric Frame. Recall, the Taxon system permits animals to approach landmarks irrespective of their position.

According to the Geometric Module theory, landmarks or features are *"pasted"* onto the Metric Frame, allowing circumstances involving geometric ambiguity to be resolved. Cheng (1986) and Gallistel (1990) emphasise the Metric Frame and Featural Subsystem are encapsulated, independent modules but rely predominantly on the former rather than latter for purposes of navigation. It is the independency of these modules which implies competition should not occur between landmarks and geometric information. Hence, in situations where the location of a goal is described by geometric as well as featural cues; competition between these cues should not occur. The Geometric Module can thus be used to predict that landmarks should not overshadow or block learning based on the macroscopic shape of the environment.

1.07 Organisation of this Thesis

The overall purpose of the current work was to assess the claim made by Cheng (1986) and Gallistel (1990) that information about the shape of an environment is stored in a dedicated Geometric Module, impenetrable to featural cues such as landmarks. To achieve this goal I have taken an unconventional approach and divided the thesis into two parts. In Part I, an effort is made to provide an answer to the question "are cue competition effects such as overshadowing and blocking evident between landmarks, and if so can similar interactions be observed between the overall shape of an environment and a featural cue placed within that environment?" The aim of Part II is to assess whether animals use the cues surrounding a hidden goal in a global way as Cheng (1986) and Gallistel (1990) argue, or whether they use them in a more local or restricted fashion instead. Part II, shall follow the empirical work of Part I.

In Part I attention shall be directed first to experiments relevant to the theory of the Cognitive Map (O'Keefe & Nadel, 1978). Many of these studies have required animals to find a hidden goal with reference to cues located either inside or outside a maze (see Chamizo et al, 1985; Redhead et al, 1997). For the present purposes these cues shall be referred to as intramaze and extramaze cues respectively. Such a distinction is completely arbitrary, but it is nonetheless helpful for organising the many experiments that have been conducted in this area. I shall begin by citing studies that have examined occurrences of overshadowing and blocking between intramaze and extramaze cues. This shall be followed by evaluating whether these same cue competition effects might also be observed in situations where the location of a hidden goal is described exclusively either by extramaze or intramaze cues.

I then move on to consider whether featural and geometric cues compete for the control they acquire over behaviour. If there is any hint of cue competition between these cues then the proposals made by Cheng (1986) and Gallistel (1990) would be brought into question, whilst at the same time lend support to the Rescorla- Wagner Model (1972). I begin by citing studies to show apparent failures of an intramaze landmark to overshadow learning based on the shape of an environment with enclosed walls. Experiments relevant to this issue have used rectangular and non-rectangular shaped apparatus and the former shall be considered before the latter. An examination of blocking will follow. Regrettably, only two studies have tested whether pre-training with an intramaze landmark might block learning based on the distinctive shape of an environment. Even so, it is worthwhile including these studies because there are empirical (Kamin, 1969) and theoretical (Rescorla & Wagner, 1972) grounds to suppose that blocking is a more powerful test of cue competition than overshadowing; and if there is an absence of blocking then this would pose serious problems for the Rescorla-Wagner Model (1972).

If there is any generality to the proposals made by Cheng (1986) and Gallistel (1990) then it is logical to assume that extramaze cues might also fail to restrict learning based on the shape of an environment with enclosed walls. Regrettably, few studies have been designed with this idea in mind. They shall nevertheless be evaluated because they form the justification for the experiments included in Chapter 3.

Another body of research has examined if the presence of a distinctive featural cue might restrict learning based on the shape described by a configuration of landmarks. If competition should occur in these circumstances it would extend the conditions under which failures to observe cue competition occur, whilst also extending the generality of the ideas expressed in the theory of the Geometric Module (Cheng, 1986; Gallistel, 1990). Rather disappointingly, discussion will have to be limited to overshadowing because not one study to date has examined if pre-training with an intramaze landmark might block learning based on the shape of a landmark array.

1.08. Overshadowing Between Intramaze and Extramaze Cues

Chamizo et al (1985) were the first to assess whether cue competition, and in particular overshadowing could be found in spatial learning. They used a three-arm radial maze. The first arm, from which rats were always released, was made of plain wood. The floors of the remaining arms were covered in different textures, sandpaper or rubber, and these surfaces functioned as intramaze stimuli. The features of the experimental room surrounding the apparatus acted as extramaze stimuli. All animals were required to retrieve food hidden at the end of a textured arm. For two experimental groups, Compound-I and Compound-E, the food remained in a stable position with respect to the cues surrounding the maze. Moreover, it always occupied an arm with the same texture throughout training- the one with the rubber-textured floor for example. These groups could thus find food by referring to the intramaze as well as the extramaze cues.

Subsequent to training, tests were conducted during which food could be retrieved from both textured arms. For Group Compound-I the arms of the maze were placed in new positions with respect to the room cues, making them irrelevant for searching. Rats were thus forced to rely upon the intramaze cues for finding the food during the test. Unfortunately, their preference for searching in the correct arm was rather poor compared to that of a control group trained to find food with reference to just the intramaze cues. It therefore appears that for Group Compound-I the presence of the room cues during training restricted the control acquired by the intramaze cues.

In contrast to the above conclusion the experiment provides no hint of overshadowing of the extramaze cues by the ones inside the maze. Group Compound-E was also given a test trial. For them the arms of the maze occupied the same positions to that used for training. For the test food was available in each textured arm, but they were covered in identical surfaces. Rats thus had to identify the correct arm during the test by referring to the room cues but not the textures. The results showed that rats preferred searching in the correct arm as did a control group for whom the room cues were relevant for finding food during the training stage.

Taken together the results provided by Chamizo et al (1985) suggest that the intramaze cues were overshadowed by but did not overshadow learning based on the extramaze cues. In a more recent study using a similar design to that of Chamizo et al, March, Chamizo and Mackintosh (1992) revealed a reciprocal overshadowing effect: extramaze cues overshadowed intramaze cues and vice versa.

A study conducted by Redhead et al (1997) also illustrates the degree to which intramaze and extramaze cues interact. They used rather different apparatus to that of Chamizo et al (1985). In one experiment three groups of rats were trained to escape onto a submerged platform from a circular pool filled with opaque water. The platform remained in a stable position with respect to the cues surrounding the pool and Group Beacon was trained with two different beacons visible above the waterline. One beacon was directly above and attached to the platform whilst the other was located some distance away from it. Rats could therefore locate the platform by referring to either the beacon above it or the cues surrounding the pool. According to the Rescorla-Wagner model (1972), these conditions are sufficient to result in the beacon overshadowing learning about the position of the platform relative to the room cues. Group Pilot was also trained with two beacons, but they were identical. The room cues but not the beacons thus indicated unambiguously the platform's location. A control group was trained without a beacon in the pool. They were therefore reliant upon the room cues for identifying the location of the platform.

After successfully completing the training stage, rats were given a test trial conducted in the absence of the beacons and the platform but in full view of cues surrounding the pool. Results showed that Groups Pilot and Control, but not Group Beacon searched in the region of the pool previously occupied by the platform. On the basis of this outcome Redhead et al (1997) argued that the distinctive features of the beacon overshadowed learning based on the room cues. This result adds to the generality of the results reported by Chamizo et al (1985).

Despite their obvious differences, the studies conducted by Chamizo et al (1985) and Redhead et al (1997) suggest that overshadowing can occur between cues located inside a maze with those located outside. I now turn to consider whether blocking can also be found between these cues.

1.09. Blocking Between Intramaze and Extramaze Cues

One of the first studies to reveal a blocking effect was conducted by Chamizo et al (1985). They used the three-arm radial maze mentioned earlier and as before rats were trained to find food hidden at the end of a textured arm. In the second stage of the experiment all animals were treated identically. Food not only remained in the same textured arm but also in a stable position with respect to the room cues. Rats could thus identify the position of food by referring to either the intramaze or the extramaze cues.

The two experimental groups received pretraining prior to their commencing Stage 2. For Group Intramaze, food was hidden in the arm with the same texture as that used for the second stage. Even so, its position with respect to the room cues varied randomly for each trial, which thus made them irrelevant for finding food. As a result it is possible that learning to locate food with reference to the texture in Stage 1 might block learning based on the room cues in Stage 2.

For Group Extramaze food occupied the same place with respect to the room cues in stage one as it did for the second stage. The goal arms, however, were interchanged in a random sequence so that food occupied either the rubber or sandpaper-textured arms (see above). Hence, only the room cues were relevant for finding food throughout stage one. Thus learning to find food with reference to the room cues in the first stage might prevent Group Extramaze learning about the significance of the textures in the second stage.

At the end of Stage 2, rats were given a test trial during which food could be found in both goal arms. The correct arm was considered to be the one that contained food during the second stage. For Group Intramaze, texture was made irrelevant during the test because the goal arms were covered with the same surface. However, the spatial relationship between the correct arm and room cues was identical to that used for Stage 2. Rats could therefore search in the correct arm by referring to the room cues. Their preference for searching in the correct arm was poor compared to a control group which did not receive any pretraining. It is apparent then that pre-training with the intramaze cues blocked learning based on the room cues in the second stage.

For Group Extramaze, the arms of the maze were placed in new positions with respect to the room cues during the test. The two goal arms differed in texture but the correct arm was covered with same surface as Stage 2. Rats could thus search the correct arm by referring to intramaze stimuli. The results of the test revealed that rats searched the correct arm on fewer occasions than a control group which did not receive any pre-training, but did received Stage 2 training. Learning based on the room cues in Stage 1 thus seems to have prevented rats from learning about the importance of the textures in Stage 2. Taken together the results of Chamizo et al (1985) suggest that learning based on the intramaze cues blocked and was blocked by the extramaze cues.

Using rather different apparatus to that of Chamizo et al (1985), Redhead et al (1997) also provide evidence of blocking in a spatial task. They trained rats to escape from a circular pool, filled with opaque water, by swimming to a submerged platform which had a beacon attached to it. Throughout Stage 1 Group Beacon was trained with two different beacons. The first was attached to and directly above the platform, whilst the other was located some distance away. The beacons, and hence the position of the platform, were moved randomly between two quadrants of the pool. As a result the cues surrounding the pool were of little use for identifying the position held by the platform. Instead escape from the pool was possible by referring to the beacon above the platform. Group Pilot received similar pre-training to that of Group Beacon, except for them two identical beacon's were used and the platform remained in a stable position with respect to the room cues. Thus, Group Pilot could predict accurately the location of the platform by referring to the room cues rather than the beacons.

For Stage 2 and for both groups the platform was beneath the same beacon as it was for the previous stage, but was placed in a novel location with respect to the room cues. During this stage then, it was possible for rats to locate the platform with reference to either the beacon or the room cues. Redhead et al (1997) reasoned that Group Beacon should continue to rely upon the beacon for finding the platform in stage two because this cue was effective for escaping from the pool in the first stage. Similarly the authors also expected Group Pilot to persist with using the room cues in Stage 2 because they were helpful for finding the platform in the Stage 1.

Subsequent to Stage 2 a test trial, during which rats were allowed to swim freely, was conducted without the platform and beacons but in full view of the cues surrounding the pool. The outcome of the test showed that Group Pilot spent significantly more time than Group Beacon searching in the region of the pool occupied by the platform during Stage 2. This outcome suggests that for Group Beacon the presence of the beacon in Stage 1 blocked learning based on the room cues in Stage 2.

At first sight the results of the above studies (Chamizo et al, 1985; Redhead et al, 1997) seem to lend support to the idea that competition and in particular blocking can be found in spatial tasks. Unfortunately, it is possible to explain the above results by appealing to attentional rather than associative changes (Mackintosh, 1975; Pearce & Hall, 1980; Sutherland & Mackintosh, 1971). Recall, during Stage 1 Chamizo et al (1985) trained Group Intramaze to find food by referring to the texture associated with the correct arm, the position of which varied with respect to the room cues that surrounded the maze. The spatial relationship between the texture and food was thus stable but that between the room cues and food was unstable.

Mackintosh (1973) has argued that stimuli irrelevant to the occurrence of reward will receive less attention than if they are relevant- the learned irrelevance effect. As a result the attention that Group Intramaze directed toward the room cues would be expected to decline as Stage 1 training progressed because they were irrelevant for finding food. Consequently, it is unlikely rats would have attended to the room cues at the outset of Stage 2 and thus fail to use them cue to find food. This situation was reversed for Group Extramaze. They might have learned that texture was irrelevant for finding food during Stage 1 and paid little attention to this cue in the second stage. If there is any merit to these proposals then the poor performance of the experimental groups during the tests can be explained by the failure of rats to attend to the irrelevant stimulus during the first stage. Of course a similar account can be formulated to explain the results supplied by Redhead et al (1997).

Fortunately the outcome of a study conducted by Roberts and Pearce (1999) is difficult to explain by referring to less attention being directed to an initially irrelevant cue. Using similar apparatus to that of Redhead et al (1997), Roberts and Pearce (1999) pre-trained two groups of rats to escape onto a submerged platform with a beacon attached to it. During this stage curtains were drawn around the pool, occluding cues in the experimental room. Subsequent training took place in full view of the room cues and rats were once again required to find the platform with a beacon attached to it. For the duration of Stage 2 the platform remained in the same place so that it was possible for rats to identify its position with reference to the room cues. For Group Block, however, such learning might be prevented by the continued presence of the beacon because it was identical to that used for the first stage. In contrast, the beacon given to the control group in Stage 2 was different to one used for Stage 1. There is thus no reason to suppose that the training given to these rats in Stage 1 should influence the associability of the room cues for finding the platform in Stage 2.

To assess the above predictions rats were given a test trial conducted in full view of the room cues, but without the platform and beacon. As expected, Group Block spent significantly less time than Group Control searching in the area of the pool previously occupied by the platform. It is unlikely that rats behaved in this way due to an effect similar to learned irrelevance (Mackintosh, 1975) because the room cues were occluded by the curtain during pre-training.

The results provided by Roberts and Pearce (1999) appear to show that pre-training with the beacon in Stage 1 and its continued presence in Stage 2 prevented Group Block from learning about the significance of the room cues. There is, however, one rather simple alternative explanation for their results. It is possible that Group Block focused so much attention on the beacon in Stage 1 that they failed to notice the addition of the room cues in Stage 2. It is no wonder then that rats found it difficult to find the platform with reference to just the room cues during the test. This issue is considered further, following the discussion of the next three experiments.

1.10. Overshadowing Among Extramaze Cues

So far discussion has focussed on the interaction between intramaze and extramaze cues. Another body of research has focussed entirely on competition among extramaze cues. One experiment to reveal an overshadowing effect between cues of this type was conducted by Sanchez-Moreno, Rodrigo, Chamizo, and Mackintosh (1999). They trained rats to find a submerged platform located in a circular pool filled with opaque water that was surrounded by four distinctive landmarks, A, B, C and D. For one group, but not the other, an auditory stimulus, X, was presented in the same spatial location as D and Sanchez-Moreno et al (1999) suspected that the presence of X might restrict learning based on D. To assess this prediction a number of tests were conducted with a subset of three landmarks but without the platform. Control tests, carried out with landmarks A, B and C showed that the groups did not differ and searched in the region of the pool previously occupied by the platform. However, the group trained with the auditory cue, X, spent significantly less time than the control group searching in the correct region of the pool when tested with landmarks A, B and D. It thus seems that the presence of X restricted learning based on D. Despite the plausibility of this conclusion the outcome of the test trial can be explained more simply by arguing that the group trained with the auditory cue, X, experienced a greater generalisation decrement than the group trained without X. Hence the claim that X restricted learning with reference to D must be taken with caution.

1.11. Blocking Among Extramaze Cues

Notwithstanding the above criticism the study conducted by Sanchez-Moreno et al (1999) raises the possibility that extramaze landmarks compete with each other for the control they acquire over searching for a goal. Rodrigo, Chamizo, McLaren and Mackintosh (1997), who used a blocking design, have tested this idea further. They used similar apparatus to that of Sanchez-Moreno et al (1999), but used a visual rather than an auditory stimulus as the blocking cue. During pre-training, Group Block was required to find a submerged platform that remained in the same place with respect to three landmarks A, B and C that surrounded the pool. Throughout Stage 2 the platform remained in the same place and a fourth landmark, X, was added to the landmark array so rats could identify the position of the platform with reference to all four landmarks. Learning based on the added landmark, X, however, might be blocked by the presence of the three original landmarks. The control group was treated identically to Group Block throughout the second stage but did not receive any pre-training. As a result this group was expected to base their search for the platform on all four landmarks A, B, C and X during Stage 2. Testing took place in the presence of a subset of three landmarks but without the platform. Control tests, conducted with the original three landmarks, A, B and C, revealed Groups Block and Control did not differ and spent considerable time searching in the quadrant of the pool previously occupied by the platform. However, when tested with landmarks, A, B, and X, Group Block spent significantly less time than the control group searching in the correct area of the pool. On the basis of this result Rodrigo et al (1997) argued that pre-training Group Block to locate the platform with reference to the three landmarks, A, B and C, blocked learning about the added landmark, X.

1.12. Blocking among Intramaze Cues

Other experiments have examined if competition might occur between intramaze cues. One such study was undertaken by Biegler and Morris (1999) who used an open field task and adopted an elaborate three stage blocking design. The first and final stages of the experiment shall be described first because for these stages the groups were treated identically. During Stage 1, rats were required to find food located at the apex of an imaginary triangle (see figure 1.01).

Two identical landmarks, A and A' were located at the corners at the base of a triangle and the angle between each corner at its base and food was 45 degrees. The entire array was rotated between trials and a black curtain surrounded the apparatus to limit the influence of extraneous stimuli. Under these conditions the landmarks provided ambiguous information about where to search for food: describing two possible locations. The first of which was the location already described whilst the second was in the reflected position if a mirror was placed along the triangle's base.

During Stage 3, rats were trained with landmarks A, A', as well as two new landmarks that were different from each other and the originals. The first landmark, B, was located on the right-hand side of the array whilst the second landmark, C, occupied a left-hand position. Rats could thus use landmarks B and C throughout Stage 3 to search for food in the correct place rather than in the reflected position. However, during Stage 2 Group Block received pre-training with landmark B in the position it appeared for Stage 3: making it possible for rats to predict accurately the location of food with reference to A, A' and B. The possibility thus remains that landmark B might block learning based on landmark C due to the continued presence of B in the third stage.

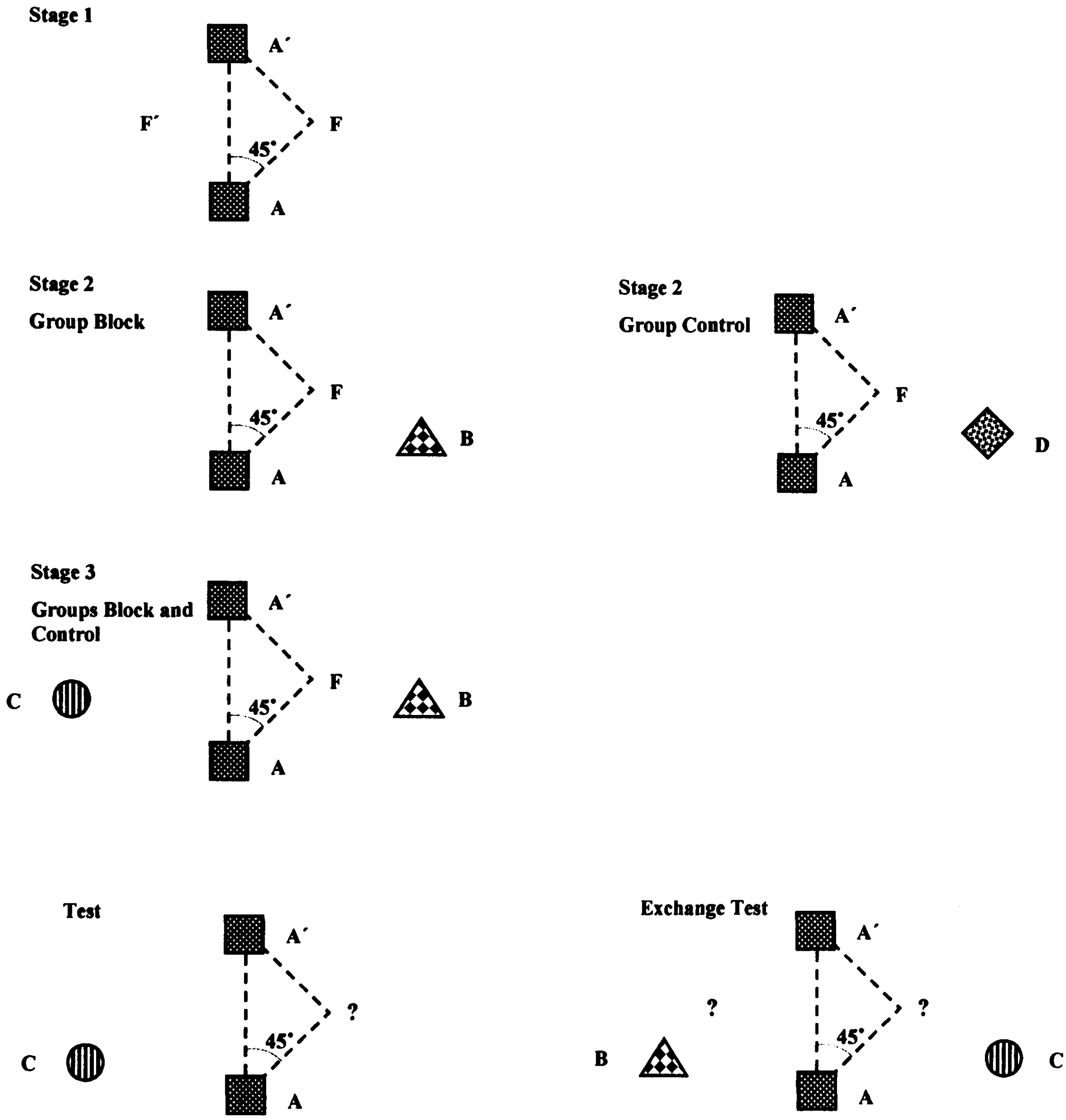


Figure 1.01 Schematic representation of the apparatus used by Biegler and Morris (1999). The shaded geometric shapes represent landmarks. F denotes the position of food whilst F′ indicates the geometrically equivalent position. The question marks show possible search locations.

Unlike the blocking group, Group Control was trained with landmark, D, during Stage 2 and this landmark was not present in Stage 3. Accordingly, there are no grounds for supposing Stage 2 training should influence what rats learned about landmarks B or C during the final stage of training.

To assess these predictions rats were given a test trial conducted without food but with landmarks A, A' and C in their prescribed locations. The outcome of the test revealed that Group Control showed a greater preference than the blocking group for searching in the area previously occupied by the food. The obvious implication of this result is that pre-training Group Block with landmark B in Stage 2 restricted learning based on landmark C in the Stage 3.

As noted earlier it is possible to explain the results of some blocking studies (Chamizo et al, 1985; Redhead et al, 1997) in terms of learned irrelevance (Mackintosh, 1973). It is, however, difficult to apply such an explanation to the results provided by Roberts and Pearce (1999), Rodrigo et al (1997) and Biegler and Morris (1999) because in these studies rats were trained with only one set of landmarks in the first stage: making it impossible for animals to learn that another set was irrelevant for finding the goal. Nevertheless, it is still possible to explain the results of the latter studies by appealing to attentional (Mackintosh, 1975; Pearce & Hall, 1980; Sutherland & Mackintosh, 1971), rather than associative changes (Rescorla & Wagner, 1972).

In the experiment conducted by Rodrigo et al (1997), for example, it is possible that Group Block failed to attend to the added landmark, X, during Stage 2 because they learned in Stage 1 that landmarks A, B and C were sufficient for finding the platform. As a result rats may have concentrated on these cues in Stage 2 and failed to notice the added landmark, D. Thus, when tested with landmarks A, B and D rats exhibited a poor preference for searching in the correct region, not because landmarks A, B and C blocked learning based on D, but because rats simply failed to attend to D during Stage 2.

Similar arguments can explain with some ease the blocking effects reported by Pearce et al (1999) and Biegler and Morris (1999). The former study has already been dealt with. In the latter study it would be somewhat superfluous of Group Block to direct any attention to the added landmark, C, during Stage 3 because rats may have learned that referring to landmark B was sufficient to search in the correct place during Stage 2. Biegler and Morris do note, however, that upon the introduction of landmark C in the third stage rats from the blocking group did explore it. Such exploration suggests that rats directed at least some attention towards C, hinting at the possibility that learning based on this landmark was in fact blocked by B, through a mechanism such as that proposed by the Rescorla-Wagner model (1972).

Notwithstanding the above criticism the study conducted by Biegler and Morris (1999) raises the possibility that whilst blocking might occur between landmarks, it certainly seems to fail between landmarks and the geometric cues provided by a landmark array. Recall, in that experiment rats were trained during the third stage with two distinctive landmarks, B and C. They occupied positions to the right and left, respectively, of two identical landmarks, A and A'. For one test, conducted without food, the authors exchanged the landmark on the left with the one on the right of the array. And surprisingly the groups, who did not differ, showed a considerable preference for searching in the area of the array previously occupied by food. This outcome suggests first that rats must have used the overall shape provided by the landmark configuration to find food.

Another obvious implication of the above result is that even though Group Block learned to identify the location of food by referring to landmark B in the second stage; such learning seemingly failed to restrict learning based on the overall shape of the landmark array in final stage. Similar failures of landmarks to restrict learning based on geometry shall be discussed in more detail later with reference to the theory of the Geometric Module (Cheng, 1986; Gallistel, 1990).

Blocking between intramaze landmarks is not confined to experiments with rats. Cheng and Spetch (2001) pre-trained one group of honeybees, Group Block, to find a dish of sucrose that was located to the left of a blue cylinder. During the second stage a yellow cylinder was added to the apparatus so that sucrose was positioned directly between the two landmarks. It was thus possible for the blocking group to use either cylinder to identify the position of sucrose. However, learning based on the yellow cylinder might be blocked by pre-training with the blue one. A control group did not receive any pre-training, but were treated identically to Group Block throughout the second stage. Group Control should thus learn about the spatial relationship between each cylinder and the sucrose. A test, conducted without sucrose but with the two landmarks in their original positions, showed that bees searched directly between the two cylinders for food. However, when the blue cylinder was removed Group Block spent significantly less time than the control group searching in the area previously occupied by food. Hence, pre-training honeybees to find a goal with reference to the blue cylinder in Stage 1 blocked learning based on the yellow cylinder in Stage 2.

Together the studies discussed so far make clear that competition between landmarks can be found in a variety of circumstances. Overshadowing and blocking seem to occur readily between intramaze and extramaze stimuli (Chamizo et al, 1985; March et al, 1992; Redhead et al, 1997; Roberts & Pearce, 1999). These same cue competition effects also arise between cues positioned within the intramaze environment (Cheng & Spetch, 2001; Biegler & Morris, 1999). Finally, pre-training with one extramaze cue can block learning based on other extramaze cues (see Rodrigo et al, 1997, Sanchez-Moreno et al, 1999).

According to the Cognitive Map Hypothesis (O'Keefe & Nadel, 1978) cue competition effects like the ones just described should not be observed between landmarks. The above results are thus incompatible with the proposals of O'Keefe and Nadel (1978). They are in perfect agreement, however, with the general mechanism of cue competition described by Rescorla-Wagner Model (1972). That theory and others like it (Mackintosh, 1975; Pearce & Hall, 1980) thus seem to provide an adequate explanation of how spatial knowledge based on landmarks is acquired. Indeed there seems to be nothing special about spatial learning: learning about where to respond appears to be governed by the same principles as learning about when to respond.

Results such as the one provided by Biegler and Morris (1999) suggest that competition cannot be found between landmarks and the shape described by a landmark array. This failure to observe cue competition is difficult for associative learning theories to explain (Mackintosh, 1975; Pearce & Hall, 1980; Rescorla & Wagner, 1972) but it is nonetheless compatible with the idea that animals possess an independent module for processing geometric information which is, for the most part, impenetrable to featural cues (Cheng, 1986; Gallistel, 1990). The aim of the following section is to assess these contradictory perspectives.

1.13. Absences of Overshadowing in Rectangular Environments

Unlike traditional forms of spatial learning (for example, Redhead et al, 1997; Roberts & Pearce, 1998), learning based on the shape of an environment seems to be largely unaffected by the presence of intramaze landmarks. One of the first studies to illustrate this apparent failure to find cue competition was conducted by Cheng (1986). He trained rats to find food that was buried in one corner of a rectangular arena with black walls, 38 cm high (see figure 1.02, left-hand panel). In each corner of the rectangle were placed four panels of unique texture and pattern. During a reference memory task food was always placed in the same corner and near the same panel throughout training. The panels thus described the location of food unambiguously. By comparison, due to its axial symmetry the arena described two possible corners in which to search: the correct one and its geometric equivalent. Efficient retrieval of food therefore depended on referring to featural rather than geometric cues

During tests food was available in every corner and the percentage of trials rats first searched each corner after being released into the arena was recorded. When tested with apparatus identical to that used for training, rats spent 91% of trials searching in the correct corner. In the diagonal transformation test the panels in the correct and geometrically equivalent corners were exchanged. Under these conditions rats displayed an 80% preference for searching in the geometrically equivalent corner even though it did not contain food during acquisition. Thus, during the two tests rats seemed to search with reference to the panel that originally occupied the same corner as food. And such results imply that their behaviour was controlled predominantly by featural rather than geometric cues.

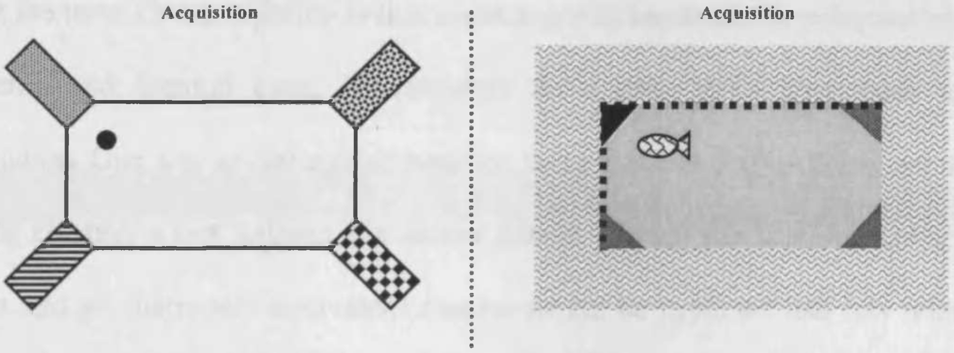


Figure 1.02. Schematic representation of the apparatus used by Cheng (1986; left-hand side) and Vargas et al (2004; Right-side panel). Each experiment used a rectangular arena. The textured panels used by Cheng (1986) are depicted by the 4 small shaded rectangles. The filled circle gives the location of food during training. The striped walls used by Vargas et al (2004) are shown by the bold dotted lines. The filled triangles denote doors fish could exit whilst the shaded triangles signify blocked doors. G indicates geometrically correct locations. F gives the location of searches guided by the feature.

In addition to the above conclusion Cheng (1986) argued that subjects must have also searched with reference to the geometry of the arena. According to Cheng evidence to substantiate this claim can be found in the results of the test trials described above. In the first test rats made more errors of searching in the geometrically equivalent corner than of errors searching in any other corner. Moreover, in the diagonal transformation test rats spent 20% of trials searching in the correct corner even though it was occupied by a panel that was different to that used for training. It is apparent then that rats searched with reference to geometric cues even though the panels described the exact location of food. For this reason it could be argued that the corner panels failed to restrict learning based on the shape of the environment.

Unfortunately, there are several limitations in the design of Cheng's study (1986) that make it difficult to be confident about the failure to observe cue competition. One problem is that rats were always tested in the presence of landmarks. It is therefore not easy to establish exactly which cue or set of cues animals were responding to during the tests. One possibility is that searching was based on the independent use of geometric and featural cues. Alternatively these cues could have been used in conjunction. One way to distinguish between these methods for searching would have been to conduct a test without the corner panels. During this test, searching in the correct and geometrically equivalent corners would be expected had rats referred to the geometry of the arena to find food. Had they instead relied on featural cues then searching in the latter corners would certainly not be anticipated. It is a pity that Cheng (1986) did not, on any occasion, test his subjects in the manner proposed. As a result any interpretation of his results is little more than conjecture. Moreover, Cheng (1986) also failed to include suitable control groups in any of his studies and this issue will be discussed in more detail with reference to similar studies that have also failed to include controls.

Results similar to those of Cheng (1986) have been provided by experiments that have used fish as subjects (Sovrano, Bisazza & Vallortigara, 2002; 2003; Vargas, López & Thinus-Banc, 2004). In one such study Sovrano et al (2001; 2002) trained fish to escape through a hidden door that was located in one corner of a rectangular pool. The pool itself was surrounded by a larger tank containing fish of the same species which, because of their being gregarious, encouraged those in the inner pool to escape (see figure 1.02, right-hand panel).

In one experiment all four walls of the pool were white and located in each corner were panels of different patterns. Thus, unlike the corners of the pool the panels described the location of the hidden door unambiguously. Throughout the experiment Sovrano et al (2001; 2002) recorded the number of trials fish attempted to escape from each corner of the pool. In the training stage fish spent more trials trying to escape through the door in the correct rather than the geometrically equivalent corner. Their behaviour must have therefore been guided, at least in part, by the corner panels. During a test without the panels they tried to escape as often from the doors in correct and geometrically equivalent corners. Crucially, escape attempts at the latter corners were substantially greater than the remaining two. Together these results suggest that the corners of the pool were not overshadowed by the panels, despite their gaining at least some control over searching during training.

Regrettably, Sovrano et al (2001; 2002) used procedures which may have inadvertently encouraged fish to adopt a method of escape that relied upon neither geometric nor featural cues. During each stage of the experiment there were four identical escape doors in each of the arena's corners. Only the doors in the correct corner and occasionally the one in the geometrically equivalent corner could be opened, the others always being blocked. Fish could therefore escape with some efficiency simply by testing which of the four doors could be opened. Such procedures would have been suitable for training but all the doors should have been open for the test because this would have then ruled out the possibility that fish adopted an escape strategy like the one described. For this reason the results of Sovrano et al are somewhat limited.

Another study to use fish as subjects was undertaken by Vargas et al (2004). This study used similar apparatus to that of Sovrano et al (2002; 2003) and goldfish were trained to escape through one of four identical doors hidden in each corner of a rectangular pool that was surrounded by a larger tank. Importantly training and testing were carried out in the manner proposed above: fish could exit the pool through any door in the test, but only through the one in the correct corner during training.

In one experiment two walls of the pool, one long the other short were white. The remaining walls were patterned with grey and white vertical stripes and these walls met in the corner occupied by the hidden escape door (see figure 1.02, right-hand panel). Thus, in comparison to the corners of the pool, the striped walls described unambiguously the location of the door.

In one test the two striped walls were replaced by two white ones, resulting in all four walls of the arena being white. In these circumstances fish searched with equal frequency the corner originally occupied by the hidden door and the geometrically equivalent corner. There was thus no indication that learning based on the rectangular pool was restricted by the presence of the striped walls. To be confident about this conclusion, though, a control group trained in the absence of the striped walls should have been included in the experiment. Such a group was unfortunately omitted, thereby restricting the implications of the results.

There is some evidence to suggest that learning based on the shape of an environment in chicks is also unaffected by the presence of landmarks. In one study Vallortigara, Zanforlin and Pasti (1990) trained 12-days old chicks to find food buried in one corner of a rectangular arena similar to that used by Cheng (1986). All the arena's walls were white and located in each corner were panels of different colours and patterns. Thus, as with the experiments already discussed, the panels but not the corners of the arena described the location of food unambiguously. Throughout training chicks successfully searched the correct corner and did not, on any occasion, search the geometrically equivalent corner. It is apparent then that the panel in the correct corner gained substantial control of chicks' behaviour.

Vallortigara et al (2004) went on to conduct a test in the absence of the corner panels and food. Prior to being released from the centre of the arena, subjects were disoriented by slowly rotating them. The results of the test revealed that chicks searched with equal frequency in the correct and geometrically equivalent corners and made very few errors of searching in the remaining corners. Thus, overshadowing of the rectangular arena by the panel in the correct corner failed, even though this featural cue acquired substantial control over searching during acquisition. Once again, however, such an interpretation needs to be taken with some caution because a suitable control group was not included.

Notwithstanding the criticisms already noted, the aforementioned experiments do suggest, albeit tentatively, that a variety of species can navigate with reference to the shape of an environment. Unfortunately, it is difficult to be confident about any of the apparent failures to find cue competition because not one of the studies mentioned so far included a suitable control group.

Recall for example, the study conducted by Cheng (1986) in which rats were trained to find food hidden in one corner of a rectangular arena that had four different panels in each corner. As a result all rats at all times were trained with two sets of cues: geometric and featural. It is therefore impossible to assess the degree to which rats learned about each cue independently. Any overshadowing effect of geometric learning by the features is thus impossible to determine. Similar problems are apparent in the studies that have used fish as subjects (Sovrano et al, 2001; 2002; Vargas et al, 2004) and the study conducted by Vallortigara et al (1990) that used chicks as subjects.

One simple method of overcoming the above problem would have been to include a control group trained with geometric but not featural cues. Such a group would show first that geometric learning could occur in the absence of features. It is not clear from any of the above studies that animals are capable of learning about the shape of an environment under these circumstances (see Cheng, 1986; Sovrano et al, 2002; 2003; Vargas et al 2004; Vallortigara et al, 1990). A control group trained without features could also be used to judge the extent to which learning based on geometry was restricted by the presence of the features in an experimental group trained with both types of cue. The absence of a control group thus makes it somewhat difficult to interpret the results supplied by the preceding experiments.

Fortunately, a study conducted by Kelly, Spetch and Heth (1998) included a control group similar to the one described above. This study can therefore be used to assess directly any overshadowing effect of the featural cues on geometric learning. They trained pigeons to find food hidden in one corner of a rectangular arena that had four white walls and this apparatus was similar to that used by other authors (Cheng, 1986; Vallortigara et al, 1990). The feature group could predict accurately the location of food because for them each corner of the rectangle was occupied by a panel unique in texture and pattern. By comparison, the control group was forced to rely on the ambiguity of the arena for finding food because for them the rectangle was devoid of features.

Subsequent to training, the groups were given a test trial conducted without the corner panels and food. The performance of the groups did not differ and birds searched with equal frequency in the correct and geometrically equivalent corners. As such there was no hint that the arena's geometry was overshadowed by the corner panels in groups trained with them. Moreover, cue competition failed even though the panels obtained a great deal of control over searching. Indeed during a control test, conducted without food but with the panels in their allotted positions; the feature group limited their search to the correct corner, failing to make any errors of searching in any other corner of the arena.

The apparent failures to find cue competition in the studies discussed so far (Cheng, 1986; Sovrano et al, 2002; 2003; Vargas et al, 2004; Vallortigara et al, 1990; Kelly et al, 1998) is extraordinary because they all required animals to find a goal located in one corner of a rectangular arena where a featural cue was also located. As a result the feature was much more reliable than the corners of the arena for predicting the location of food. According to the Rescorla-Wagner model (1972) these are precisely the conditions under which the feature should have overshadowed learning based on geometry. Clearly this did not occur. Thus, if there is any merit to the above results, it seems that Rescorla-Wagner provides an inadequate explanation of how spatial knowledge based on the shape of an environment is acquired.

1.14 Absences of Overshadowing in Non-Rectangular Environments

All the experiments in the previous section used rectangular apparatus and provided evidence to suggest that learning based on that shape was unaffected by the presence of featural cues. Such results do not, however, rule out the possibility that features such as landmarks might restrict learning based on other shapes. One study to address this issue was conducted by Tommasi and Vallortigara (2001), who trained 8 days-old chicks to find food hidden at the centre of a square arena with walls 70 cm long and 40 cm high. Located at the arena's centre was a conspicuous red-painted cylindrical landmark. The location of food was thus described equally well by the square arena and the landmark. Theoretically (for example, Rescorla & Wagner, 1972) these conditions are sufficient to observe overshadowing.

Over the course of acquisition chicks successfully searched at the centre of the arena and after 8 days they were given a test trial conducted in the absence of the landmark and food. Contrary to predictions derived from the Rescorla-Wagner model (1972), chicks continued to search in the centre of the square during the test. Hence, the presence of the cylindrical landmark seemingly failed to restrict learning based on the geometry of the square arena.

The above conclusion needs be taken with some caution, however, because it remains possible that chicks failed to use the geometry of the square arena to search. Instead, they might have used the distance between the food and the walls of the arena as a cue to search in the centre of the square during training. Such a simple non-geometric strategy could have easily been used to search in the same place during the test. A larger square would have provided better circumstances for testing. Under these conditions searching at the centre would be expected had chicks relied on the shape of the smaller training arena to find food. Alternatively, searching away from the centre and closer to the walls of the test arena would be expected had they learned to locate food with reference to its distance from the walls of the smaller square. Tommasi and Vallortigara (2001) failed to conduct a test in a larger arena. Evidence to suggest that subjects referred to the geometric properties of the arena to find food is thus somewhat lacking. Accordingly it is difficult to assess whether or not the learning based on the arena was restricted by the presence of the landmark.

It is perhaps worth noting that Tommasi and Vallortigara (2000, 2001) have also trained chicks to find food hidden in the centre of the square arena mentioned earlier, but in the absence of a landmark. Chicks were tested in an arena larger than the one used for training. In these circumstances subjects searched in two places. The first corresponded to the distance they searched for food during training, whilst the second was the actual centre of the larger test apparatus. Chicks must have therefore relied on two different strategies to find food. As noted above searching at the arena's centre implies they referred to the overall shape of the environment. Alternatively searching closer to the arena's walls suggests chicks exploited a strategy for finding food that did not rely on the shape of the arena and was similar to the one described above. It is possible then that in the experiment conducted with the red-painted cylindrical landmark chicks could have adopted either a geometric or non-geometric strategy for finding food.

An experiment that used a rather different shape was conducted by Pearce, Ward-Robinson, Good, Fussell and Aydin (2001). They trained rats to swim to a submerged platform, located in one corner of a triangular shaped pool that had a curved base. For Group Beacon the platform remained in the same corner throughout training and attached to it was a prominent landmark, or beacon. As a result rats could find the platform by referring to either the beacon or the geometric cues provided by the corner in which it was hidden. Group Control was treated identically to the beacon group; except for them the beacon was absent. This group was therefore required to rely on the geometric cues of the correct corner for finding the platform. For the final group, Group Random, the beacon was also attached to the platform but was moved between the two corners at the base of the triangle in a random sequence over the course of training. As such rats could accurately predict the location of the platform by referring to the beacon but not the geometry of the pool.

During a test trial conducted without the beacon or platform Groups Beacon and Control, who did not differ, exhibited a strong preference for searching the correct corner, whilst Group Random failed to show any preference for searching either of the two corners at the triangle's base. On the basis of these results Pearce et al (2001) argued that for Group Beacon, the presence of the beacon failed to restrict learning based on the shape of the triangular pool. Had overshadowing been successful, then Group Beacon should have exhibited only a weak preference for searching the correct corner.

Unlike many of the experiments described earlier, the experiment undertaken by Pearce et al (2001) included a control group trained without landmarks. For reasons already discussed, this greatly facilitates the interpretation of the results. The failure of a landmark to restrict learning based on geometry found in the above experiment, however, is not as striking as previous failures to find cue competition (Kelly et al, 1998). This is because the triangular shaped pool and the beacon were equally reliable as cues for predicting the location of the platform. Had rats been trained with a rectangular shaped pool instead, the landmark would have been a more reliable cue than geometry for finding the platform. Cue competition effects are thus theoretically (Rescorla & Wagner, 1972) less likely to occur with triangular than with rectangular shaped environments and it is perhaps for this reason Pearce et al failed to observe cue competition.

1.15 Absences of Blocking in an Environment with a Distinctive Shape

To overcome the above problem it might be possible to adopt training procedures which, according to associative learning theory (Rescorla & Wagner, 1972) will restrict geometric learning to a greater extent than was theoretically possible in the previous study. One way of achieving this goal is to provide pre-training with a landmark so that blocking (Kamin, 1969) will prevent any control being acquired by the shape. In an additional experiment, Pearce et al (2001) did just that. The experimental group of rats, Group Block was pre-trained to escape from a circular pool onto a submerged platform that had the beacon fixed to it. During this stage curtains were drawn around the pool to occlude extraneous landmarks. What is more, the platform and beacon always occupied the same location in the pool for each session but were moved together to a different position at the start of a new session. As a result the blocking group was forced to rely on the beacon for finding the platform.

During Stage 2 the platform always occupied the same corner of the triangular pool mentioned earlier and once again curtains were drawn around the apparatus. It was therefore possible for the blocking group to identify the position of the platform by referring to the shape of the pool. However, attached to the platform was the same beacon as that used during Stage 1. Learning based on the shape of the pool might thus be blocked by the continued presence of the beacon during Stage 1.

Two other groups were included in the experiment. The first, Group Random, received identical training to that given to the blocking group during Stage 1. For the second stage the platform, with the beacon attached to it, was moved between the two corners at the base of the triangle in a random sequence. As a result, this group was expected to learn very little about the location of the platform relative to the shape of the pool during the second stage. A control group did not receive any pre-training, but was given training identical to that given to the blocking group for Stage 2. As a result this group was expected to learn more about the shape of the pool than the blocking group.

During a test trial, conducted in the absence of the platform and beacon, the blocking group searched in the corner of the pool previously occupied by the platform, which implies that learning based on the triangular pool in the second stage was not blocked by pre-training with the beacon in the first stage. One shortcoming of the experiment is that the control group failed to show any preference for searching in the correct corner of the triangular pool during the test, making it difficult to assess the influence of the beacon in the blocking group. However, had the beacon restricted, to any degree, learning based on geometry, the blocking group would have been expected to exhibit only weak preference for searching in the correct corner of pool during the test. Group Block nevertheless preferred searching the latter corner. There are thus sufficient grounds for supposing that cue competition failed.

Wall, Botly, Black and Shettleworth (2004) also provide an example of a failure to find blocking. In one study an experimental group of rats was pre-trained to find food that was hidden in a corner of a square arena where a black panel was also located. The panel was moved with the food in a random sequence among the corners. Rats could therefore predict accurately the location of food by referring to the panel rather than the corners of the square. Stage 2 training took place in a rectangular arena. As before rats had to find food, but on this occasion it remained in the same corner. The corners of the rectangle could therefore be used by rats as a cue to search for the food. However, for Group Block the same black panel occupied the corner containing food. The black panel in stage one and its continued presence in stage two might thus block learning based on the rectangular arena.

To test the above prediction rats were given a test trial in the rectangular arena but without the black panel or food. The outcome of the test revealed that Group Block spent a considerable amount of time searching the correct corners as did a control group that did not receive any pre-training. It is apparent then that blocking of the rectangular arena by the black panel failed.

In the above study pre-training with the black panel was undertaken in a square arena (Wall et al, 2004). Rats could thus use the arena as a cue for predicting the location of food even though it was not as reliable as the black panel. Even so, the square arena might have restricted, to some extent, the amount of control acquired by the black panel during Stage 1. As a result the black panel may have failed to block learning based on the rectangular arena in Stage 2 simply because it did not acquire sufficient control to do so. The use of a circular arena during pre-training would have easily overcome this problem. Of course, in these circumstances it would have been impossible to use a corner panel as the featural cue. Instead a beacon like the one used by Pearce et al (2001) would have been ideal.

1.16. The Interaction of Extramaze Cues and the Shape of an Environment

It seems apparent from the preceding discussion that competition between an intramaze cue and environmental geometry is rarely found. I argued earlier, however, that under some circumstances extramaze cues will restrict learning based on intramaze ones (Chamizo et al, 1985; March et al, 1992; Roberts & Pearce 1998). It remains a possibility therefore that cues located outside an enclosed environment might restrict learning based on its shape. Unfortunately not one experiment to date has been designed to test this idea directly. Nevertheless a study conducted by Margules and Gallistel (1988) illustrates that extramaze cues can at the very least acquire some control over behaviour when they as well as environmental geometry describe the location of a hidden goal.

In their experiment Margules and Gallistel (1990) trained rats to find a token that was hidden in one corner of a rectangular arena with black walls. This apparatus was housed within a large room which provided the extramaze cues. For the group of interest, the arena was completely devoid of features. Consequently, rats had to refer to the extramaze cues if they were to find the token. Over the course of training there is every indication they accomplished this because rats showed a preference for searching the correct over the geometrically equivalent corner. Whether the control acquired by the room cues was sufficient to overshadow learning based on the arena's shape is difficult to determine, however, because the experiment included neither the appropriate tests nor controls. Whilst not conclusive then, these results do leave open the possibility that extramaze cues might, under the appropriate conditions, restrict learning based on environmental geometry.

1.17. An absence of Overshadowing between a Featural Cue and the Shape of a Landmark Array

Other experiments have endeavoured to assess whether cue competition effects such as overshadowing can be found between featural cues and the shape provided by a landmark configuration. In one experiment Benhamou and Poucet (1998) trained two groups of rats to escape from a circular pool onto a hidden platform, the location of which was fixed relative to three different landmarks that were arranged to form a triangular configuration (see figure 1.03). Two landmarks, A and B were cylinders. A was taller and narrower than B and was patterned with black and white vertical, rather than horizontal stripes. The platform was placed on the North-South axis of the pool as the platform and the distance between these objects was constant. The remaining landmark, C, was a black cone. The various patterns and colours of the landmarks provided rats with featural cues they could use to distinguish between them.

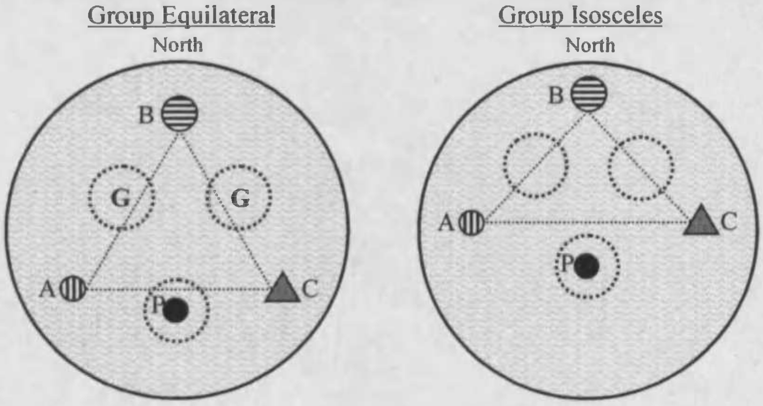


Figure 1.03. The apparatus used by Benhamou and Poucet (1998. Circles A and B signify cylindrical landmarks, having vertical and horizontal stripes, respectively. The third landmark, a cone, is given by the shaded triangle. The filled circle denotes the position of the platform. The dashed circular lines show the areas that were used to assess the performance of the rats during test trials conducted without the platform. The letters G show the two positions in the pool that were geometrically equivalent to the position occupied by the platform (P).

For Group Isosceles the landmarks formed an isosceles triangle that occupied one half of the pool. Rats could thus find the platform without reference to the featural cues because the shape of the array described its location unambiguously. For the other group, the landmarks formed an equilateral triangle. As a result the array's shape described three places in which to search for the platform, each being geometrically equivalent. In figure 1.03, P marks the actual location of the platform during training and G two alternative positions. Geometric ambiguity meant that rats had to rely on the featural cues provided by the landmarks as well as the shape they created to find the platform.

As a result of training the groups in the manner described, there are theoretical grounds (for example, Rescorla & Wagner, 1972) to suppose that learning based on the equilateral triangle might be restricted to a greater extent by the features than learning based on the isosceles triangle. Regrettably, it is not easy to assess this prediction because Benhamou and Poucet (1998) never tested rats without the featural cues. Such a test could have been carried out rather simply by replacing the three different landmarks with novel yet identical ones, arranged in the same shape as the originals. Evidence of cue competition would then be revealed by rats exhibiting a poor preference for swimming in the area of the pool previously occupied by the platform. Of course this prediction would only hold true for the isosceles group, the other group being used as a control.

Despite the above misgivings, Benhamou and Poucet (1998) provide some evidence to suggest that learning based on the shape of the array was unaffected by the presence of the features. They gave rats a test trial conducted with the landmarks in their original positions but without the platform. During this test, Group Isosceles spent more time than the equilateral group in the area of the pool previously occupied by the platform. In fact, the latter group showed the same preference for searching in each of the three geometrically equivalent regions of the pool. It is unlikely that rats based their search on cues outside the pool because a curtain surrounded it, the orientation of the apparatus was changed for each trial and rats were slowly rotated before each trial commenced.

One interpretation of the above results is that learning based on the equilateral triangle was not restricted by the presence of the featural cues. Such a conclusion has to be taken with considerable caution, however, not only for the criticism already noted, but because the experiment suffers several other design flaws.

The first concern is how the apparatus was arranged for Group Isosceles. For this group, the landmarks were always placed in the opposite half of the pool to that occupied by the platform. One effective method for finding the platform, therefore, would have been to avoid swimming in the area of the pool containing the landmarks. The results of the test trial can then be explained by this use of a simple non-geometric strategy. Hence, rats did not have to refer to the shape of the array to search. For this reason it is problematic to make comparisons between the groups.

The equilateral group may have also failed to use the shape of the array to search. Figure 1.03 shows clearly that for this group the platform occupied a position between and below landmarks A and C. Consequently rats may have swum from one landmark to another to find the platform during training and used this non-geometric strategy to search for it during the test. A strategy of this kind would then explain why rats spent the same amount of time searching in the three geometrically equivalent areas during the test. There is some evidence to suggest that rats may have in fact used this non-geometric strategy. A typical search pattern provided by Benhamou and Poucet (1998) shows that rats took a circuitous route around the pool during the test-swimming in the area between the landmarks and the pool's edge. Such behaviour implies rats adopted a strategy for finding the platform like the one described, making geometric information redundant.

Another problem with the above experiment is that there is no evidence to suggest that rats in either group used the features to find the platform. Thus, overshadowing may have been unsuccessful simply because the features failed to acquire sufficient control over searching. Benhamou and Poucet (1998) partially addressed this concern in another experiment by showing that rats were capable of discriminating between the landmarks. In that study rats were trained with the same three landmarks and again they formed a triangle. However, they did not have to refer to the shape of the array because the platform was hidden directly in front of one of the landmarks. Swimming toward the landmark was thus sufficient to escape from the pool. Each landmark was tested in this manner and the results showed that animals always approached the landmark with the platform first.

Success in the discrimination task suggests that the landmarks' features must have acquired at least some control over searching. Regrettably, demonstrating control by features in one experiment does not imply a similar level of control was acquired by the features in the other. In the absence of evidence to the contrary it is conceivable that overshadowing was unsuccessful because the features failed to acquire sufficient control over subjects' behaviour.

1.18. The Presence of Overshadowing between a Featural Cue and the Shape of a Landmark Array

In contrast to the above results, a study conducted by Spetch and Wilkie (1994) can be used to illustrate that individual landmarks rather than the shape of a landmark array can acquire control over searching for a hidden goal. In that study pigeons were trained to peck a hidden goal area of a touch screen for food. The goal area completed the fourth corner of an irregular quadrilateral described by three different landmarks (see figure 1.04, left-hand panel). The landmarks were digitized images of a tree, a flower and a log and were presented on a background of green grass. The textures and colours related to these landmarks thus provided featural cues that could be used to peck within the goal area.

The position of the goal was fixed relative to the landmarks and these objects were moved as a unit to a new location on the screen for each trial, their orientation with respect to the screen remaining constant. Consequently the location of the goal could be identified by referring to the array's shape or any of three landmarks. Spetch (1995) has shown that landmarks closer to a goal overshadow those farthest away. Thus, learning based on the flower and the log might be restricted by the tree because it was closer to the goal than they were. Moreover, the tree might also restrict learning based on the shape of the array.

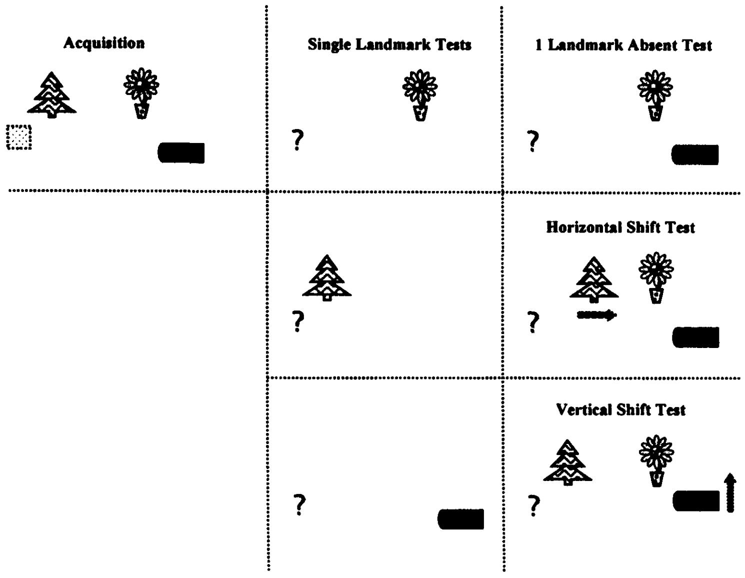


Figure 1.04. The arrangement of stimuli used by Spetch and Wilkie (1994). The landmarks were 3D images of a tree, a flower and a log and were presented on a rectangular touch screen (not shown). The left-hand panel shows the stimuli as they appeared during acquisition trials. The small shaded square depicts the hidden goal area. The remainder of the figure gives examples of the test trials. The question marks show the original location of the hidden goal box. The figure is not drawn to scale.

Upon successful completion of the training stage, birds were given a number of non-reinforced test trials during which they were presented with modified versions of the original array. In one series of tests each landmark was presented separately on the screen in its prescribed location. Under these conditions pigeons searched in the correct area; but only when the tree was displayed. Moreover, when tested with an array missing one landmark or tested with one landmark shifted horizontally across the screen to a new position, pigeons search accuracy declined in response to the removal or shift of the tree and no other landmark.

Taken together the above results suggest that neither the flower or log, or even the shape described by the landmark array controlled searching for the goal. Had searching been based on the array's shape then removing just one landmark would have been sufficient to disrupt pecking accuracy. Of course search accuracy did decline, but only in response to the removal or shift of the tree. The latter landmark thus appears to have restricted learning based on the individual landmarks as well as the shape they described.

To the best of my knowledge this is the first example of the apparent success of a landmark, albeit a two-dimensional one, to disrupt spatial learning based on the shape of a landmark array. It is perhaps worth noting that because Spetch and Wilkie (1994) used an irregular quadrilateral, the tree and the array's shape were equally reliable as cues for predicting the location of the goal- conditions which are theoretically sufficient to observe overshadowing (Rescorla & Wagner, 1972). Unfortunately, it is difficult to confirm this apparent success of cue competition because neither a control group nor an appropriate test in which the original landmarks were replaced with novel yet identical ones, were included in the study. The implications of the results supplied by Spetch and Wilkie (1994) are therefore somewhat limited.

One study to include a control group was undertaken Garrad-Cole, Lew, Bremner and Whitaker (2001). They required 18-24 months-old infants to find a toy that was hidden inside one of four corner boxes arranged to form a rectangle measuring 6 x 4 ft. The toy was always hidden in the same box throughout the experiment. Infants saw the toy being hidden, were slowly rotated with their eyes closed, and then asked to retrieve it.

For Group Identical each box was the same and uniformly white. There was thus no method by which infants could disambiguate the correct box from its geometric equivalent. For Group Different the boxes were unique in colour. These infants could therefore use colour as a cue to predict accurately the toy's location.

Over the course of training Garrod-Cole et al (2001) recorded the number of trials infants searched in each box. The results showed that Group Identical searched equally often in the correct and geometrically equivalent boxes, suggesting they referred to the shape of the array. By comparison Group Different searched predominantly in the correct box, all other searches being evenly distributed between the remaining three boxes. There was thus no hint that these infants used the geometry of the array to search. Had they done so, a small bias for searching in the box geometrically equivalent to the one with the toy would have been observed. Such a bias was completely absent which implies the features of the box containing the toy must have acquired considerable control over searching. Once again, however, it is not easy to judge whether this control was sufficient to restrict learning based on the array because Group Different was never tested in the absence of the featural cues.

1.19. Aims and Objectives of Part I

Contrary to the claims made by O'Keefe and Nadel (1978), one firm conclusion to draw from the previous review is that spatial learning based on landmarks seems to obey the same laws that are known to govern Pavlovian conditioning (for example, Mackintosh 1975; Pearce & Hall, 1980; Rescorla & Wagner, 1972). Evidence of overshadowing (Chamizo et al, 1985; Redhead et al, 1997) and blocking (Rodrigo et al, 1997; Roberts & Pearce, 1999) between landmarks supports this point of view.

Whether a similar conclusion can be reached about all forms of spatial learning remains uncertain. According to the proposals of Cheng (1986) and Gallistel (1990) learning based on the shape of an environment should be unaffected by the presence of landmarks. Unfortunately, many of the studies designed to test that theory have been poorly designed, making it difficult to assess whether geometric and featural cues compete for the control they acquire over searching. The primary purpose of Part I was to rectify this situation. Accordingly all the experiments were designed with associative learning theories in mind (Mackintosh 1975; Pearce & Hall, 1980; Rescorla & Wagner, 1972).

At first sight the apparent failures to find competition between geometric and featural cues poses problems for theories like the Rescorla-Wagner model (1972). However, if the featural cues were found to be much less salient than the geometry of an environment then it follows from a number of theories that the former should not restrict learning based on the latter (For example, Mackintosh, 1975; Pearce & Hall, 1980; Rescorla & Wagner, 1972). Chapter 2 is particularly relevant to this explanation for the failures to detect cue-competition.

With the exception of two experiments (Pearce et al, 2001; Wall et al, 2004) the majority of studies described earlier used overshadowing designs. There are empirical (Kamin, 1969) and theoretical reasons (Rescorla & Wagner, 1972) to suppose that blocking is a more sensitive test of cue competition than overshadowing. Thus providing pre-training with a landmark might prevent any control being acquired by the shape of an environment. Experiments 2 and 3 were based on blocking designs. They thus provide particularly stringent conditions under which to test predictions derived from theory of Geometric Module (Cheng, 1986; Gallistel, 1990) as well as the Rescorla-Wagner model (1972).

Although there is a great deal of evidence to suggest that featural and geometric cues fail to compete for the control they acquire over searching; there may still be situations in which cue competition might be observed between these cues. One possibility is that a landmark might restrict learning based on the shape of a landmark array. Regrettably, existing studies have made it difficult to be sure about this claim. Experiment 4 was designed with this issue in mind. Another reason for conducting Experiment 4 was to test further the possibility mentioned earlier that the failures to detect cue competition may have resulted from the landmark being of low salience relative to the distinctive shape of an environment.

Even if pre-training with a landmark should fail to block learning based on the shape of an environment; it is plausible that such learning might be influenced by the presence of other cues such as those provided by an experimental room. There is sufficient evidence to suggest that the presence of room cues can overshadow intramaze cues (Chamizo et al, 1985). Furthermore Margules and Gallistel (1988) have demonstrated that room cues can control searching for a goal hidden in one corner of a rectangular arena, but this study was not designed with cue competition in mind. The main purpose of Chapter 3 was to test whether the presence of room cues might overshadow learning based the distinctive shape of an environment and vice versa. Once again the issue of stimulus salience is discussed.

Throughout the introduction I have assumed that overshadowing will always occur when two stimuli are presented in compound (Kamin, 1969; Pavlov, 1927). Durlach and Rescorla (1980) have, however, shown that in some circumstances conditioning with a compound stimulus comprising two CSs can result in learning based on one of them becoming potentiated. Potentiation can thus provide one way in which to account for the repeated failures of the landmark to restrict learning based on the shape of an environment (Cheng, 1986; Kelly et al, 1995; Pearce et al, 2001). Experiment 7 was designed to test if a landmark might potentiate learning based on the shape of swimming pool, whilst Experiment 8 explored possible mechanisms for this effect.

Chapter 2.

Failures of an Intramaze Landmark to Restrict Spatial Learning based on the Distinctive Shape of a Pool.

In the introduction I argued that similarities could be found between Pavlovian conditioning and the acquisition of spatial knowledge based upon landmarks. Evidence of overshadowing (Chamizo et al, 1985; Redhead et al, 1999) and blocking (Roberts & Pearce, 1999; Sanchez-Moreno et al, 1999) between landmarks lends considerable support to this conclusion. Associative learning theories (Rescorla & Wagner, 1972), but not theories of spatial learning (O'Keefe & Nadel, 1978), thus seem to provide an adequate explanation of how spatial knowledge based on landmarks is acquired.

By comparison there seems to be very few situations in which cue competition can be found between the distinctive shape of an environment and any landmark placed within that environment (Cheng, 1986; Kelly et al, 1998; Pearce et al, 2001). These failures to observe cue competition are not easy for associative learning theories (Rescorla & Wagner, 1972) to explain. They are, however, perfectly compatible with theories of spatial learning (Cheng, 1986; Gallistel, 1990). Hence, there seems to be something fundamentally different about the acquisition of spatial knowledge based on landmarks and that based on the shape of an environment.

Even though there is a great deal of evidence to suggest that learning based on the shape of an environment is unaffected by the presence of landmarks (Cheng, 1986, Kelly et al, 1998; Pearce et al, 2001; Tommasi & Vallortigara, 2000) it might still be possible for associative learning to explain these failures to find cue competition. Reconsider for a moment the experiment conducted by Pearce et al (2001) in which rats were trained to find a submerged platform located in one corner of a triangular-shaped pool: the correct corner. For the experimental group a landmark was attached to the platform. Consequently the shape of the pool as well as the landmark described unambiguously the location of the platform. These two cues were thus equally reliable for escaping from the pool. According to associative learning theory (Rescorla and Wagner, 1972) such conditions are sufficient to demonstrate overshadowing. Even so, there was no hint that learning based on the geometry of the pool was restricted by the presence of the landmark (Pearce et al, 2001). Such an outcome raises at least two possibilities. First, it is plausible that the method of training designed to result in the landmark becoming an effective cue for overshadowing was unsuccessful. It also possible that the test employed to reveal the effects of cue competition was not sufficiently sensitive.

One way to increase the effectiveness of the landmark as a cue for overshadowing is to adopt training procedures which, according to associative learning theory, will restrict the degree of learning about the shape of the pool to a greater extent than learning based on the landmark. A possible method of achieving this goal is to ensure that the shape of the pool is less reliable than the landmark as a cue for predicting the location of the platform. To this end Experiment 1 used a rectangular shaped pool and rats were trained to find a platform hidden in one of its corners, where a landmark was also located. Due to the rectangle's axial symmetry, the pool contained two possible corners in which to search for the platform. The first was the corner occupied by the platform whilst the other was the corner geometrically equivalent to it. In contrast, the landmark described unambiguously the corner in which to search for the platform. The corners of the rectangular pool were thus less reliable than the landmark as cues for predicting the location of the platform. Accordingly, associative learning theory (Rescorla & Wagner, 1972) anticipates the corners of the pool should acquire less control over searching for the platform than the landmark. Hence, the landmark should, at least theoretically, become a more effective cue for finding the platform than the geometry of the pool. The likelihood of geometric learning being restricted by the presence of the landmark in this study is therefore greater than in the study conducted by Pearce et al (2001).

Another method to restrict the degree of learning based on shape of the pool is to provide pre-training with a landmark so that blocking (Kamin, 1969) will prevent any control being acquired by geometry. Experiments show that such pre-training with a landmark blocks spatial learning based upon other landmarks (Roberts & Pearce, 1998). Such pre-training might, therefore, also block spatial learning based on the distinctive shape of an environment. There is very little evidence, however, to support this point of view. Both Pearce et al (2001) and Wall et al (2004) have conducted experiments in which animals were pre-trained to find a hidden goal with reference to a single landmark. For Stage 2 the goal occupied one corner of an arena with a distinctive shape: the correct corner. The geometry of the arena could thus be used to find the goal. The landmark, which animals were pre-trained with, also occupied the correct corner. As a result learning based on the landmark in Stage 1and its continued presence in Stage 2 might be expected block learning based on the shape of the arena.

Contrary to above prediction animals persisted searching in the correct corner during tests without the landmark which implies animals learned to locate the goal with reference to the shape of the arena. In short there was no evidence that geometric learning was blocked by pre-training with the landmark. This conclusion is of course based on a null result from just two studies. In order to lend support to the conclusion drawn from these studies there is a need to confirm the absence of blocking within the domain of geometric learning using a variety of designs and Experiments 2 and 3 were designed to address this issue.

Finally it might also be possible to explain the failures to detect cue-competition between featural and geometric cues in terms of associative learning theory by referring to the salience of the landmark. If the salience of the landmark was much less than of the shape of the pool, then it follows from a number of theories (Mackintosh, 1975; Pearce, 1994; Rescorla & Wagner, 1972) that the landmark will be relatively ineffective for overshadowing. Experiments 2 and 3 are of direct relevance to this explanation for the failure of a landmark to overshadow the control acquired by the shape of an environment. Experiment 4 explored the issue of stimulus salience further. In that study four identical cylinders were used to create a rectangle, a manipulation that was intended to reduce the salience of geometric cues relative to featural cues. If the salience of the rectangle was greatly reduced then it would, according to Rescorla-Wagner model, increase the effectiveness of the landmark as a cue for overshadowing.

2.01. Experiment 1

As noted above, under circumstances where the corner of the pool is a less reliable cue for finding the platform than the landmark, the landmark might be expected to overshadow learning based on the shape of an environment. The first experiment is a direct test of this idea. Three groups of rats were trained to find a submerged platform that was always located in one corner of a rectangular shaped pool filled with opaque water. The design of the experiment is summarised in figure 2.01. To restrict the use of cues outside the pool for finding the platform, curtains surrounded the arena and its orientation was changed for each trial.

For an experimental group, Group Landmark, a landmark was located in close proximity to the platform. This group could therefore use the landmark to identify unambiguously the location of the platform. In contrast, the shape of the pool provided ambiguous information about where the platform was hidden because there was no difference between the corner containing the platform and the geometrically equivalent corner. Thus, for Group Landmark, the landmark was a more reliable cue for finding the platform than the corners of the pool. Under these conditions theories of associative learning (Rescorla & Wagner, 1972) predict that the landmark should restrict the extent to which the shape of the pool is used to find the platform.

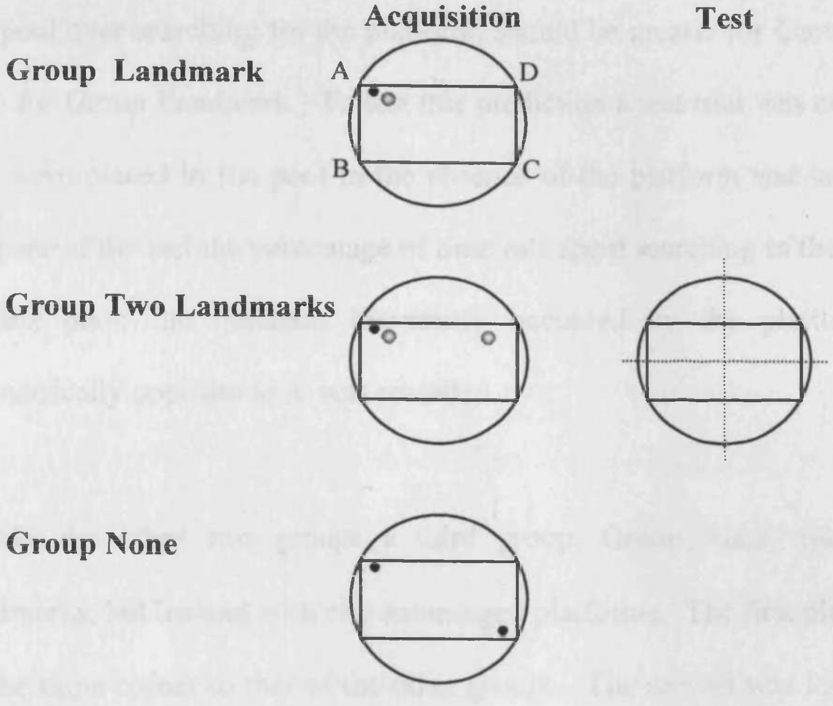


Figure 2.01. The design and apparatus used for experiment 1. The location of the platform is given by the filled black circle. The shaded circles show the positions occupied by the landmarks. The letters A, B, C and D were used to label the corners of the rectangle depicted in the figure. Corner A was the geometrically correct corner and C the geometrically equivalent corner. During the test all the objects were removed from the pool (right-hand column).

A control group, Group Two Landmarks was trained in a similar manner to Group Landmark, except that these rats were trained in the presence of two landmarks. One landmark was located near the platform and in the same position as the one used to train Group Landmark. The other landmark, which was identical to the first, was located in an adjacent corner. However, the corner chosen for the additional landmark comprised different geometric properties to the one with the platform. For example the second landmark occupied the corner with the short wall to the right of the long wall when the platform occupied the corner of the pool in which these characteristics were reversed. As a consequence the landmark was no more reliable than the shape of the pool as a cue for finding the platform. Theories of associative learning (Rescorla & Wagner, 1972) predict that the control acquired by the shape of the pool over searching for the platform, should be greater for Group Two-landmarks than for Group Landmark. To test this prediction a test trial was conducted in which rats were placed in the pool in the absence of the platform and landmarks. For the purpose of the test the percentage of time rats spent searching in the correct quadrants of the pool: the quadrant previously occupied by the platform and the one diametrically opposite to it, was recorded.

Unlike the other two groups a third group, Group None, was trained without landmarks, but instead with two submerged platforms. The first platform was located in the same corner to that of the other groups. The second was located in the corner diametrically opposite to the one with the platform. The reason for including this group was to assess the degree to which rats used the shape of the arena, in the absence of landmarks, to find the platform. Two platforms rather than one were used so that this group like the others would have the opportunity of being able to swim directly to a corner occupied by a platform on every training trial.

Finally, the experiment used a sphere, visible above the surface of the water, as the landmark. The centre of the sphere was 30 cm from the centre of the platform, which in turn was 30 cm from the corner of the pool. One reason for using this landmark was that Roberts and Pearce (1998) found it to be an effective cue for overshadowing spatial learning based on extramaze cues. Another reason for using the sphere was that rats found it difficult to climb which reduced the likelihood of its acquiring any conditioned properties other than the ones intended.

Method

Subjects The subjects were 30 male Hooded Lister rats *(Rattus norvegicus)* supplied by Joint Services of Cardiff University. They had previously participated in an appetitive Pavlovian conditioning experiment for which they had been reduced to 80% of their free-feeding weights. They were allowed unrestricted access to food and water for two weeks prior to the start of the present experiment, and for the duration of the experiment itself. All the rats were housed in pairs, in a room that was illuminated for 14.5 hr each day. The rats were tested 5 days a week, at the same time each day and at a time when the lights were usually on in their holding room. At the start of the experiment the rats were randomly assigned to the three groups.

Apparatus The pool was circular, 2 m in diameter and had a depth of 1 m. It was white, made from fibreglass and mounted on a platform 0.6 m above the floor in the middle of a room, which was 4.0 m x 3.0 m and 2.3 m high. The pool was filled to a depth of 27 cm, with water, and was rendered opaque by adding 0.5 l of white opacifier E308 that was supplied by Roehm and Haas (UK) Ltd (Dewsbury). The water and the opacifier were changed daily, the water being maintained at 25°C (+/-2 C°). A video camera with a wide angled lens was placed 1.75 m above the centre of the pool and the camera's lens was situated 25 cm above a 30-cm diameter hole in a white circular ceiling, with a diameter of 2 m. The image from the camera was relayed to recording equipment. The rats' movements were analysed using Watermaze software (Morris and Spooner, 1990). In the circular ceiling above the pool were eight 45-watt spot lights 22.5 cm in diameter that were arranged at equal distances in a circle with a diameter of 1.6 m. The spotlights were illuminated throughout the experiment. The escape platform, which was made from clear Perspex, was 10 cm in diameter and was mounted on a column. The surface of the platform was composed of a series of concentric ridges. The column stood on the floor of the pool and the platform surface was 2.5 cm below the surface of the water. The landmarks, which were identical, were plastic spheres with a diameter of 13.0 cm. Each sphere was painted white on the top half and black on the bottom half. A rigid rod attached each sphere to a metal plate that rested on the floor of the pool. The lowest part of the sphere was 2.0 cm above the surface of the water. A light-blue curtain, 1.4 m in height, hanging from the ceiling, was drawn completely around the pool, and fell 25 cm beyond the pool's 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, running 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. The door was open throughout the experiment and allowed access to an adjacent room where the experimenter remained throughout each trial and where it was possible to observe the pool and the rats' behaviour on a TV monitor.

Four white Perspex boards were suspended vertically in the pool from bars which extended over the pool edge. There were two long boards and two short boards. The long boards were 1.8 m in length, 0.59 m high and 2 mm thick. The short boards were 0.9 m in length and of the same height and thickness as the long boards. The long boards extended 33 cm above the surface of the water, whilst the short boards, because they rested on top of the short boards extended 35 cm above the surface of the water. When all the boards were placed into the pool they were used to form a rectangular arena that was 1.8 m in length and 0.9 wide.

Procedure Rats were transported to a room adjacent to the test room five at a time in light tight boxes, which were placed on a shelf. All rats received 12 sessions of training. There were four trials in each session, and for each trial rats were required to escape from the pool by swimming to the submerged platform. If a rat failed to find the platform within 90 s, the experimenter placed a finger approximately 5 cm in front of the rat's nose and guided it to the platform. Rats were allowed to remain on the platform for 30 s before they were removed from the pool. After a trial, the rats were dried gently and returned to the light tight box where they waited until the other four rats had received a single trial in the pool. This cycle was repeated until all rats had received four trials. After the five rats had each received a single trial, the rectangular arena was rotated either clockwise or anticlockwise. The rectangle was always oriented along a North-South or East-West axis, where North for the sake of the experiment, was defined as the point directly opposite the middle of the room's entrance. The sequence of rotations was varied randomly from session to session and the rectangle could move through more than 90^o in one rotation. The pool was rotated from trial to trial and surrounded by a curtain in order to minimise the influence of all cues outside the pool.

Rats were released into the pool from the centres of each of the rectangle's walls and were lowered gently into the water facing the wall. The sequence in which they were released varied randomly from session to session with the constraint that each release point was used once for each session.

During acquisition trials, Group Landmark and Group Two Landmarks were required to escape from the pool by swimming to a single platform that was in either one of two geometrically equivalent corners. The centre of the platform was 30 cm away from the corner on an imaginary line that bisected the rectangle. For half of the subjects in each group the platform was placed in the corner with the short wall to the left of the long wall. For the remaining subjects the other corners were used. Within a session, the platform was located twice in each of the geometrically equivalent corners, in a random sequence. For both groups, a landmark was situated on an imaginary line bisecting the rectangle with its centre 30 cm from the centre of the platform. A second landmark was located in the pool for Group Two Landmarks. It was in an equivalent position to the first landmark, but in the corner at the end of the long wall that was adjacent to the corner containing the platform. Group None was required to escape from the pool by swimming to one of two platforms that were located in geometrically equivalent corners. Half the subjects in this group were trained with the platforms in one pair of geometrically equivalent corners and the other half were trained with the platforms in the other pair of geometrically equivalent corners. The centres of each platform were located 30 cm from their respective corners on a line that bisected the rectangle.

On every trial a record was taken of which corner a rat entered first after being released into the pool. For the purposes of this measurement, an entry into a corner was deemed to have taken place when the subject's snout entered a quadrant of a circle, with a radius of 40 cm and with its centre at the point where the walls met, in the relevant corner of the rectangle. For the sake of clarity, the corner containing the platform shall be referred to as Corner A and its geometric equivalent as C. The remaining corners were labelled B and D (see figure 2.01).

For each training trial the time taken for a rat to reach the platform, after it had been released, was measured with a stopwatch. The stopwatch was started when the rat was placed in the pool and stopped when the rat, was observed on the TV monitor, to climb on the platform. In Session 12, the first four trials were conducted in the same manner as all other training trials. On the fifth, test trial the platform(s) and landmark (s) were removed from the rectangular shaped pool. A novel release point, located at the centre of the pool, was used for the test trial and rats were allowed to swim freely for 60 s. After the test they were led to a corner of the pool previously occupied by the platform, removed from the pool and gently hand dried with a towel. The path taken by the rats during the 60-s test trial was recorded and analysed by using Watermaze software. For the purposes of this treatment, the pool was divided into four quadrants of equal area and the time spent in each of the quadrants was measured. A rat was regarded as searching in the correct region of the pool whenever it entered the quadrant previously occupied by the platform or its geometric equivalent. For half the rats the correct quadrants corresponded to the North-West and South-East quadrants of the pool whilst for the remaining half they were the North-East and South-West quadrants of the pool.

Results and Discussion

A Type 1-error rate of p<0.05 was adopted for all statistical tests in this chapter. The groups' mean escape latencies for acquisition trials from the 12 sessions of the experiment can be seen in figure 2.02.

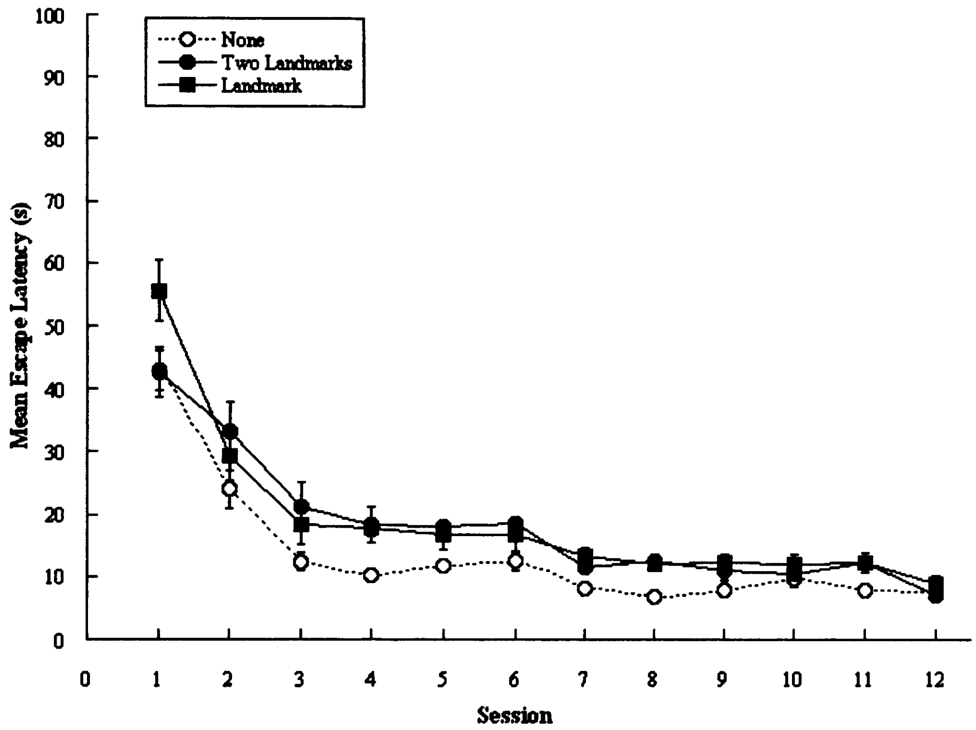
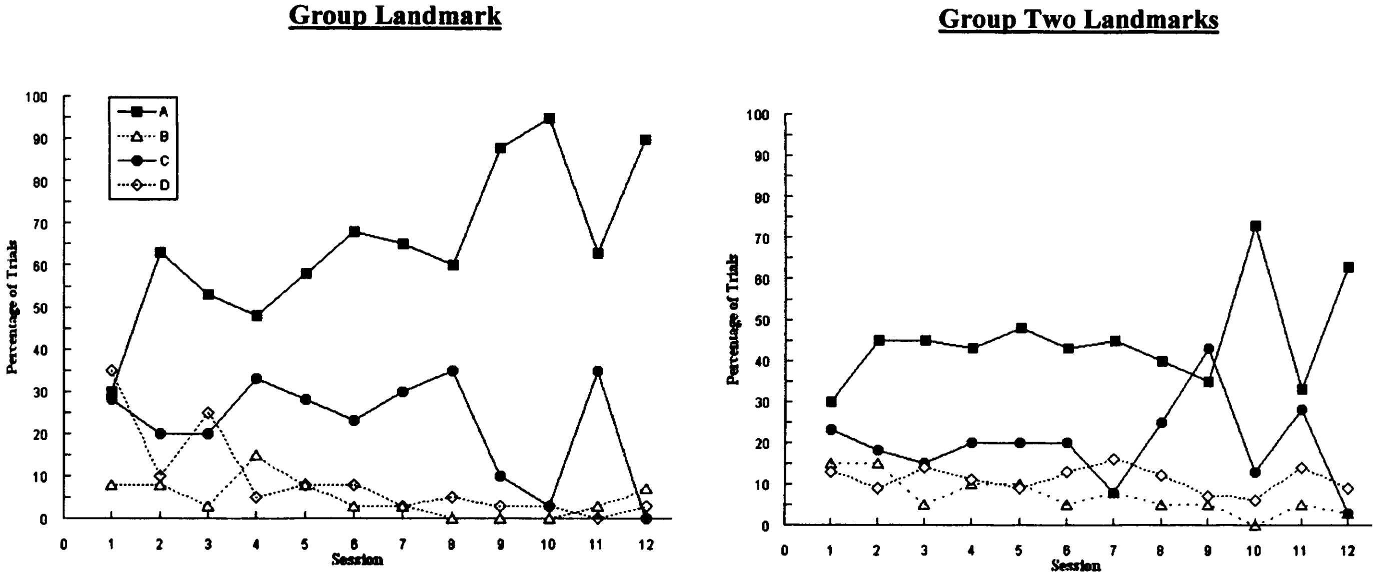


Figure 2.02. Mean escape latencies for the groups during the acquisition stage of Experiment 1 (error bars indicate ± 1 standard error).

Generally Group None was quicker to find the platform than the other two groups across sessions. The escape latencies of Groups Landmark and Two-Landmarks were similar across sessions except for the first where Group Landmark was markedly slower to escape from the pool than Group Two Landmarks. A mixed two-way analysis of variance (ANOVA) of escape latencies over the 12 sessions for the three groups, showed significant main effects of group, F(2, 27)= 9.34, Mse= 103.48, p= 0.00, η_p^2= 0.41, and of session, F(11, 297)= 83.75 Mse= 43.65, p= 0.00, η_p^2= 0.97, but the interaction of Group x Session was not significant, F(22, 297)= 1.48, Mse=

43.65, p= 0.08, η_p^2= 0.86. Tests of simple main effects showed that Groups Two Landmarks and Landmark did not differ in the time they took to find the platform, F(1, 27)= 0.27, Mse= 103.48, p= 0.61, η_p^2= 0.01. In confirmation of the observation noted above, Group None was significantly quicker to find the platform than either of the latter two groups, F(1, 27)= 18.37, Mse= 103.48, p=0.00, η_p^2= 0.41. The Sheffé procedure was used to correct the critical value of F for each of the simple main effects. One explanation for the shorter escape latencies of Group None is that every time rats swam toward a geometrically correct corner they found one of the two platforms located in these corners and escaped from the pool. For the other two groups, escape from the pool was not possible on every occasion they swam to a geometrically correct corner because only one platform was present during training. In fact rats from Groups Landmark and Two Landmarks sometimes swam toward the corner geometrically equivalent to the one with the platform first (see figure 2.03). Geometric errors of this kind presumably lengthened escape latencies for rats trained with the landmarks in comparison with Group None. Nonetheless regardless of the superiority that Group None showed, escape latencies had declined for all three groups by the end of training which suggests that rats learned to use the geometric properties provided by the rectangular shaped pool to find the platform or they may have become more adept at using the landmarks.

As well as recording escape latencies, on every trial a record was taken of which corner a rat entered first, after being released into the pool. This was done to assess the extent to which rats used the geometric properties of the rectangular shaped pool to escape onto the platform (see figure 2.01). For Groups Landmark and Two Landmarks corner A contained the platform and corner C was geometrically equivalent to the one just described, but was not occupied by a platform. Corner D represents the corner occupied by the second landmark that Group Two Landmarks was trained with. Finally one platform was situated in each of corners A and C for Group None. The percentage of trials on which the groups first entered each corner of the pool after being released was calculated for every session.



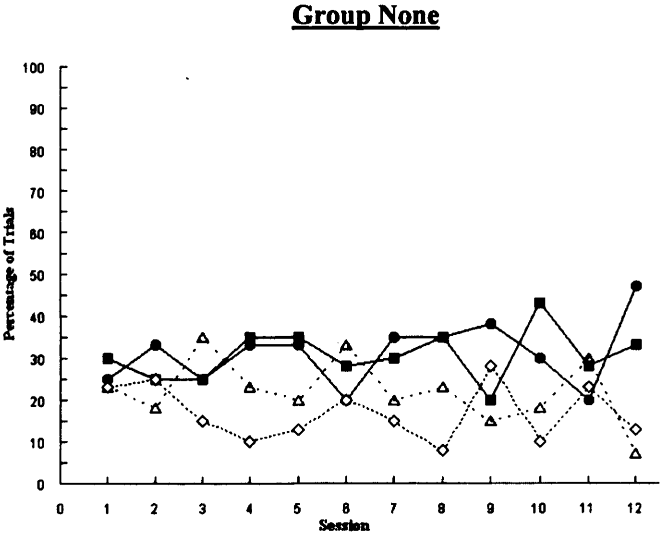


Figure 2.03. Mean percentages of trials the Groups entered first each corner of the rectangular pool during training. The performance of Group Landmark is shown in the top-left-hand corner, Group Two-Landmarks in the top-right-hand corner and Group None in the bottom left-hand-corner.

Figure 2.03 (top-left-hand corner) shows the mean percentage of trials on which Group Landmark first entered each of the four corners after being released into the rectangular shaped pool. On being released into the pool this group swam directly to the corner occupied by the platform and landmark, corner A, on the majority of trials in every session except the first. This observation strongly suggests that rats learned to use the landmark to identify the corner containing the platform. On the remaining trials subjects generally preferred to swim to the corner that was geometrically equivalent to the one containing the platform. It seems then, that rats used the geometric properties provided by the shape of the pool to find the platform, despite the presence of the landmark. There were very few occasions, particularly towards the end of training, when the remaining corners were chosen first. To evaluate these observations, within group comparisons were made between the mean numbers of trials that each corner was entered first, over all the sessions combined. The comparisons revealed that the corner containing the platform was entered first significantly more often than any other corner, Wilcoxon Ts(10)=0, and that the corner geometrically equivalent to the one containing the platform was entered first significantly more often than either of the other two corners, Ts(10)=0. These comparisons show first that rats must have used the rectangular shaped pool to find the platform. This is because rats sometimes confused the geometrically equivalent corner with the one containing the platform. Second, rats successfully disambiguated the corner with the platform from the corner diametrically opposite to it and since each of these corners comprised identical geometric properties rats must have used the landmark to do so.

Figure 2.03 (top-right-hand corner) shows the equivalent results for Group Two Landmarks and reveals that rats swam, on the majority of trials, directly to the corner where the platform was located. This observation indicates that Group Two-Landmarks used the shape of the pool in addition to the landmark for finding the platform. There was also a slight tendency for this group to swim directly to the corner of the pool occupied by the second landmark, located in corner D rather than corner B. Rats presumably searched D because it contained a landmark identical to the one located in the corner with the platform. In addition, as with Group Landmark, Group Two Landmarks swam frequently to the corner geometrically equivalent to the one with the platform (corner C), which suggests they used the geometric properties provided by the shape of the pool to escape onto the platform. Trials on which rats swam directly to the remaining corner were relatively rare.

In support of the observations made above, comparisons of individual mean percentages of trials on which rats swam directly to a particular corner, for the 12 sessions combined, revealed that the corner with the platform was chosen significantly more often than any of the other corners, Ts(10)=0. The corner geometrically equivalent to the one with the platform was chosen significantly more frequently than the two remaining corners, Ts(10)≤6. Finally the corner with the landmark, but without platform (corner D), was chosen significantly more frequently than the fourth corner (corner B), T(10)=0. These findings confirm the general observations noted above and show importantly that as with Group Landmark, Group Two-landmarks used the shape of the pool and the landmark to escape from the pool.

Finally, Figure 2.03 (bottom-left-hand corner) shows the mean percentages of trials on which Group None swam directly to the corners A and C where the platforms were located, and to the remaining corners of the pool. As training progressed there was an improvement in the percentage of trials on which this group swam directly to the corners with the platforms. A comparison of individual mean percentages of trials on which subjects swam to corners that did, or did not, contain a platform revealed a significant preference for corners with a platform, $\underline{T}(10)=9$ (one-tailed test). Thus, Group None successfully discriminated the correct corners, where the platforms were located from the remaining corners of the pool and this suggests that rats used the shape of the rectangular arena to escape from the pool.

The mean percentages of time spent in the correct quadrants of the pool over the entire 60-s of the test trial are shown in figure 2.04. One sampled t-tests revealed that the groups spent significantly more time than would be expected by chance (50%) searching in the correct quadrants of the pool during the test. These results were: $\underline{t}(9)=2.25$, $p=0.026$, for Group None; $\underline{t}(9)=3.62$, $p=0.003$, for Group Two Landmarks; and $\underline{t}(9)=4.07$, $p=0.001$, for Group Landmark. The preference that Group Landmark showed was numerically greater than that of the other two groups and Group None seemed to show the least preference.

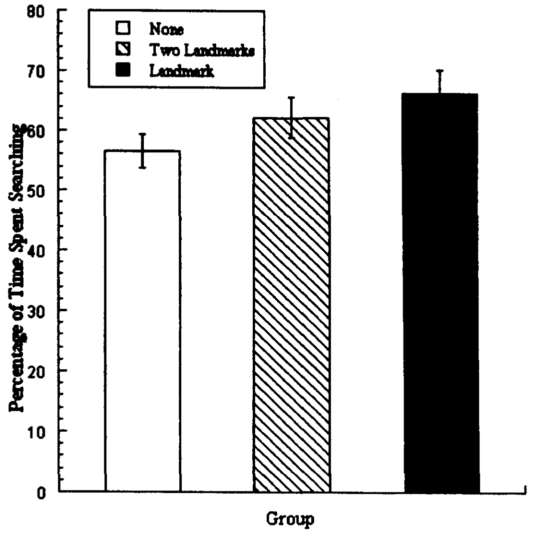


Figure 2.04. <u>Mean percentage of time the groups spent searching in the correct quadrants of the rectangular pool during the test without the platform and landmark/s (error bars indicate ± 1 standard error).</u>

Contrary to first sight a one-way ANOVA of time spent in the correct quadrants showed that the differences among the groups was not significant, F(2, 27)= 2.06, p= 0.15, Mse= 241.20, η_p^2= 0.13. The apparent superiority of Group Landmark was therefore nothing more than numerical. Importantly these results show that the landmark failed to restrict learning based on the corners of the rectangular pool in Group Landmark.

Before discussing the implications of the results for Group Landmark it is perhaps important to establish that both Groups None and Two Landmarks used the shape of the rectangular pool to find the platform. Evidence that the aforementioned groups used the geometry of the pool to find the platform is provided by the training and test stages of the experiment. Although not obvious from figure 2.03 (bottom-left-hand corner), the results from the training stage for Group None make it clear that these rats successfully disambiguated the correct corners, occupied by platforms, from the two remaining corners of the pool that did not contain platforms. In fact over all the sessions combined Group None swam to a geometrically correct corner on 64.5% of trials, a figure which is above that expected by chance. Moreover, this group also spent significantly more than 50% of its time searching in the corners of the pool previously occupied by the platforms during the test trial. Together these results unequivocally show that Group None relied on the geometric properties of the pool to find the platform.

Similarly, the results of the training stage show that Group Two Landmarks searched in the correct corner of the pool more frequently than the remaining corners of the pool. Rats also made more errors of searching in the corner geometrically equivalent to the one occupied by the platform than any other corners B or D, which suggests they confused the corner occupied by the platform with the geometrically equivalent corner that was not occupied by a platform. To make such errors rats must have relied on the geometry of the arena to navigate around the pool. In confirmation of this idea Group Two Landmarks, over all the sessions combined swam to a geometrically correct corner on 61.5% of trials, a figure which is similar to that achieved by Group None and is also higher than that predicted by chance. In addition Group Two Landmarks spent 62% of its time searching in the correct quadrants of the pool during the test and this figure was significantly more than expected by chance alone. Together these results can be taken as clear evidence to suggest that Group Two Landmarks used the shape of the pool to find the platform. Thus, even though the two control groups, Groups None and Two Landmarks, received markedly different training each group nevertheless learned to locate the platform with reference to the corners of the rectangular pool.

Now that is has been established that Groups None and Two Landmarks each used the shape of the pool to escape onto the platform the implications of the results for Group Landmark can be discussed. Like the other two groups there is abundant evidence that Group Landmark also used the shape of the pool to find the platform; even though a landmark was positioned in close proximity to the platform throughout training. This evidence is apparent in the results from the training stage which revealed that rats made more errors of swimming directly to the corner geometrically equivalent to the one with platform, than of swimming directly to the remaining other two corners. Had rats used only the landmark to swim to the platform, errors of the type just described should not have occurred. Group Landmark's use of geometry is also apparent in the results from the test trial in which rats exhibited a significant preference for swimming in the correct rather than the incorrect quadrants of the pool.

Moreover, the results of the test trial for Group Landmark show that the landmark failed to restrict learning to locate the platform with reference to the shape of the pool. Numerically, this group spent more time than the other groups searching in the correct quadrants of the pool during the test trial. The apparent absence of competition between the cues took place despite the fact that the landmark was a more reliable cue for finding the platform than the corners of the pool. And under these conditions theories of associative learning (Rescorla & Wagner, 1972) predict landmark control to be considerably greater than the control acquired by the shape of the pool. In short, the experiment provided the conditions necessary to observe an overshadowing effect of the landmark on learning based on the geometry of the pool. The landmark nevertheless failed to prevent rats from learning where the platform was located with respect to the rectangular arena. The present results are thus inconsistent with predictions derived from associative learning theory (Rescorla & Wagner, 1972); yet they are in perfect accord with the theory of the geometric module (Cheng, 1986; Gallistel, 1990) which asserts that the geometric properties of an environment are processed independently of featural information, like landmarks, and thus competition between the two sets of cues should not occur.

It might informative to consider what implications the present results have for the configural theory of associative learning proposed by Pearce (1987; 1994; 2002). As discussed in Chapter 1, Pearce assumes that when animals are conditioned with two or more stimuli in compound the overall pattern of stimulation evoked by the compound will become associated with the US. Unfortunately the present results supply rather little evidence in favour of this idea. If it is assumed that the geometric cues provided by the correct corner, A, and the landmark, B, represent two elements of a compound stimulus, AB, then it follows from configural theory that the training given to Group Landmark will have been sufficient for the configural unit of AB to become associated with the platform. In comparison the geometrically equivalent corner never contained the landmark or platform. The configural unit formed by swimming towards the geometrically equivalent corner must have therefore been markedly different from the one formed at the correct one, making them relatively easy to discriminate. The results of Group Landmark, however, revealed that rats often swam to the geometrically equivalent corner, which implies that they never completely discriminated this corner from the correct one. The results of Experiment 1 are thus difficult to reconcile with the configural theory advocated by Pearce.

The results of the test trial showed that in comparison to Group Landmark, Group Two Landmarks showed only a weak preference for searching the correct over the incorrect quadrants of the pool. One interpretation of this finding is that removing two landmarks for the test caused a greater generalisation decrement than removing just one which impaired the performance of Group Two Landmarks. Evidence to temper this idea, however, is provided by the outcome of the test trial for Group None which displayed the weakest preference for swimming in the correct quadrants despite being trained without landmarks. The inferior performance of the two control groups during the test suggests, perhaps, they learned rather little about the shape of the pool and for this reason it could be argued that they fail to provide a suitable benchmark to assess the influence of the landmark in the experimental group. There is sufficient evidence to the contrary, however. Not only did Groups Two Landmarks and None each swim to a geometrically equivalent corner on over 60% of trials (over all the sessions combined), they also spent more than 50 % of their time in the correct quadrants during the test. Together these data confirm that the two control groups learned to locate the platform with reference to the shape of the pool.

Before leaving the discussion it might be informative to compare the results of Experiment 1 with those reported by Pearce et al (2001). Recall in that experiment the experimental group was trained to find a submerged platform, with a landmark attached to it, located in one corner of a triangular-shaped pool. Under these conditions the corner of the pool and the landmark were equally reliable as cues for finding the platform. As noted above for the equivalent group in the present experiment the landmark was more reliable than the corners of the rectangular pool as a cue for finding the platform. Accordingly orthodox theories of learning (Rescorla &

Wagner, 1972) predict the effects of cue-competition to be much greater in Experiment 1 than in the one conducted by Pearce et al (2001). For this reason the failure of a landmark to restrict learning based on shape of an environment observed here is more striking, theoretically, than the failure reported by Pearce et al (2001).

2.02. Experiment 2

Experiments 2 and 3 were based on blocking designs. In each experiment a blocking group was trained first to swim to a platform near a landmark in a pool of one shape and second, to a platform near the same landmark in a pool with a different shape. The initial training with the landmark was intended to prevent, or block (Kamin, 1969), spatial learning based on the shape of the pool during the second stage of each experiment. For Experiment 2 training was conducted first, in a rectangular pool and then in a triangular pool; whereas for Experiment 3 the sequence with which rats received training in the different shaped pools was reversed.

Experiment 1 showed with some certainty that the landmark failed to overshadow learning based on the rectangular shaped pool in Group Landmark. Accordingly it was argued that the failure to observe cue-competition could be best explained by theories of spatial learning and in particular the theory of the Geometric Module (Cheng, 1986; Gallistel, 1990). However, there are theoretical (Rescorla & Wagner, 1972) and empirical (Kamin, 1969) reasons for believing that blocking designs are a more powerful technique for revealing cue competition than experiments that use overshadowing designs. It could thus be argued that Experiment 1 failed to reveal the effects of cue competition because the overshadowing design adopted was not sufficiently powerful. To overcome this problem the next two experiments used blocking designs and might therefore be regarded as providing particularly sensitive tests for assessing a disruptive influence of the landmark on spatial learning based on the shape of an environment.

One reason for conducting two blocking experiments was that if they should both reveal the same outcome, the conclusions drawn from them will be more forceful than if only one experiment had been conducted. Moreover, the results from the first stage of each experiment will enable conclusions to be made regarding the saliency of the landmark relative to the shapes of the pools. To avoid needless repetition the issue of stimulus salience shall be discussed in more detail after the results of the experiments have been described.

There were three groups of rats in Experiment 2 and each was trained first in a rectangular pool with two identical landmarks and two platforms (see figure 2.05). During Stage 1 Groups Block and None were treated identically. For these groups the landmarks were always placed in the same corners as the platforms and these objects always occupied geometrically equivalent corners of the pool. The corners containing the platform varied randomly from trial to trial, so that rats could use the landmarks but not the shape of the pool to predict accurately where the platforms might be found. For a third group, Group Overshadow, the two platforms were also placed in geometrically equivalent corners of the pool but remained in the same corners throughout the first stage. The two landmarks were also placed in geometrically equivalent corners. On half of the trials they were in the same corners as the platforms, but during the remaining trials they occupied the other corners. Thus the shape of the pool, but not the landmarks, could be used to predict accurately locations occupied by the platforms.

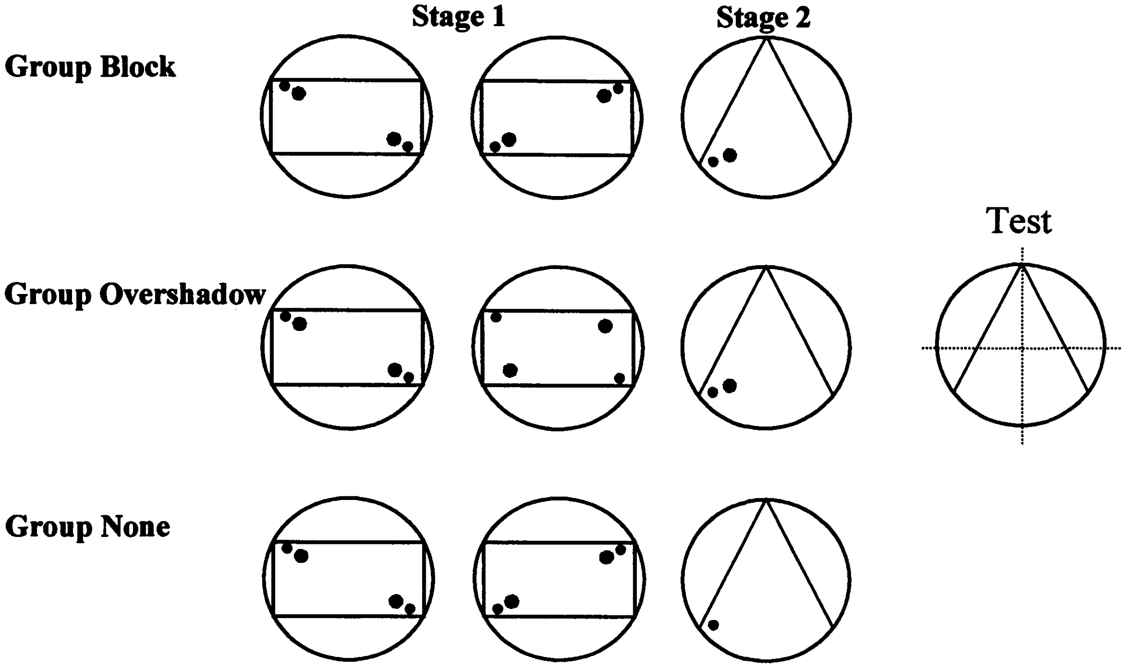


Figure 2.05. The design and apparatus used for Experiment 2. The filled black circles show the locations of the platforms. The shaded circles give the positions of the landmarks. Stage 1 training took place in the same rectangular pool used for Experiment 1 (left-hand column). Stage 2 training (centre-column) was undertaken in the triangular-shaped pool used by Pearce et al (2001). During the test all the objects were removed from pool (right-hand column).

During the second stage of the experiment a triangular pool was used and was constructed by suspending, from the edge of the pool, the two long boards used to fabricate the rectangular shaped pool of Experiment 1 (see figure 2.05, centre column). All three groups were required to find a single submerged platform that was located in one corner at the base of the triangle. There was a landmark, identical to the one used in the previous stage, near the platform for the overshadowing and blocking groups but not for the control group.

Pre-training Group Block to escape from the pool during Stage 1 should have ensured that the landmarks became effective cues for finding the platform. As a result, Group Block might be expected to rely on the landmark to identify the whereabouts of the platform at the outset and throughout the second stage. Rats could also identify the position of the platform by referring to the shape of the pool, because it remained in the same corner of the triangular apparatus throughout the second stage. Theories of associative learning theory (Rescorla & Wagner, 1972) suggest, however, the rats are unlikely to adopt the latter strategy for finding the platform because pre-training with the landmark during Stage 1 will prevent, or block any control from being acquired by the shape of the pool over searching for the platform during Stage 2.

Like the blocking group, Group Overshadow was also trained with the landmark located in the same corner of the triangular pool as the platform throughout the second stage. However, because this group was not pre-trained to find the platform with reference to the landmark during Stage 1, the landmark at the outset of the second stage should not be a reliable cue for finding the platform. The presence of the landmark during Stage 2 should thus restrict to a lesser degree, than for the blocking group, the degree of control acquired by the shape of the pool. Even so, based on predictions that can be derived from associative learning theory (Rescorla & Wagner, 1972) it is possible that the landmark might overshadow learning based on the triangular-shaped pool. Finally, the absence of the landmark for the control group should permit the shape of the pool to gain substantial control over searching for the platform.

The experiment concluded with a test trial that was conducted in the triangular pool without either the platform or landmark. If the above predictions are correct, the control group should exhibit the strongest preference for searching in the corner previously occupied by the platform, the overshadowing group should exhibit a weaker preference, and the blocking group should fail to show a preference for either corner at the base of the triangle. It must be remembered that the predictions made thus far are derived from associative learning theories like the Rescorla and Wagner model (1972). On the basis of the results obtained from Experiment 1 and with the theory of the Geometric Module (Cheng, 1986; Gallistel, 1990) in mind, there are reasons for believing that the landmark might fail to overshadow and block learning based on the triangular-shaped pool. If cue competition should fail then an equally strong preference for searching in the corner of the pool previously occupied by the platform might be observed for all groups during the test trial.

Method

Subjects and Apparatus The 29 rats were of the same stock, with similar experience, of approximately the same age, and housed in the same conditions as those of the previous experiment. At the start of the experiment they were randomly assigned to the three groups, with 10 rats in the blocking and overshadowing groups and 9 rats in the control group. For the first stage of the experiment, the apparatus and landmark were the same as for Experiment 1. During the second stage the two long boards, of 1.8 m that were used to construct the rectangle of Experiment 1, were used to form a triangular arena that had a curved base (see figure 2.05). The distance between the corners of the triangle at its base was 1.6 m. At the apex of the triangle one board extended 33 cm above the surface of the pool, whilst the other, because it was resting on top of the first extended 35 cm above the surface of the water. At the base of the triangle, each board was rested on top of the pool's edge and were thus 33 cm above the surface of the water.

Procedure For the 12 sessions of the first stage of the experiment, all three groups were required to escape from the rectangular pool by swimming to one of two platforms that were located in geometrically equivalent corners. Training took place in the presence of two landmarks that were also located in geometrically equivalent corners of the pool. For the overshadowing group the platforms remained in the same corners. The two landmarks were located in the same corners as the platforms for half of the trials and for the remaining trials they were in the corners unoccupied by a platform. For Groups Block and None the position of the platform varied randomly from trial to trial between adjacent corners of the pool. For these groups the two landmarks always occupied the same corners of the pool as the platform and were thus moved with the platforms between adjacent corners of the pool throughout training. The position of the landmarks, and hence the platforms for Groups Block and None, was changed randomly between adjacent corners for each group with the constraint that a landmark occupied each corner of the pool for two trials of every session. The centre of each platform was located 30 cm from a corner on a line that bisected the rectangle and the centre of each landmark was located on the same line, but 60 cm from a corner. Half the rats in the overshadowing group were trained with the platform located in the corners with the long wall to the right of the short wall and the remaining rats were trained the platform in the other corners. Procedural details that have been omitted were the same as for the previous experiment.

For the 12 sessions of Stage 2, the three groups were trained to escape onto a single platform that was always located in the same corner at the base of a triangular-shaped pool. The overshadowing and blocking groups were trained in the presence of a single landmark that occupied the same corner as the platform throughout training. For the remaining group the landmark was absent. The centre of the platform was 30 cm from the corner on a line that bisected the two corners at the triangle's base. The centre of the landmark was located on the same line as the platform but 60 cm from the corner of the pool. For half the rats in each group the platform was located in the left-hand corner at the base of the triangle and for the remaining rats it was located in the opposite corner. With the exception of the final session, there were four training trials in each session with rats being released from the centres of the three walls of the pool. Each wall was used at least once in every session. The triangle was rotated from trial to trial, so that its apex pointed toward North, East, South or West, in relation to the experimental room.

On every trial that took place in the triangular pool a record was taken of which corner a rat entered first after being released into the pool. For the purposes of this measurement, an entry into a corner was deemed to have taken place when the subject's snout entered a quadrant of a circle with a radius of 40 cm and with its centre in the relevant corner of the triangle. The correct corner was the one containing the platform. The corner opposite to the one with the platform was the opposite corner and the third corner was the apex.

For the final session of training there were three training trials and a single 60-s test trial. During the test the triangle was positioned so that its apex pointed North in relation to the experimental room. Rats were released from the centre of the pool and the test took place in the absence of the platform and the landmark. Procedural details of the test that have been omitted were the same as for the previous experiment.

Results and Discussion

The groups' mean escape latencies for acquisition trials that took place in the rectangular shaped pool over the first 12 sessions of training can be seen in figure 2.06 (left-hand side). Generally all groups showed a decrease in their escape latencies over sessions and between group differences were not apparent. A mixed two-way ANOVA of escape latencies over the 12 sessions for the three groups showed a significant effect of session, $\underline{F}(11, 286)= 56.92$, Mse= 49.48, $\underline{p}= 0.00$, $\eta_p^2= 0.69$. However, neither the interaction of Group x Session, $\underline{F}(22, 286)= 1.27$, Mse= 49.48, $\underline{p}= 0.19$, $\eta_p^2= 0.09$, nor the main effect of group, $\underline{F}(2, 26)= 2.80$, Mse= 73.80, $\underline{p}= 0.08$, $\eta_p^2= 0.18$ was significant. The failure to find a significant interaction suggests that conditioning with the landmark and with the geometric cues provided by the rectangular pool proceeded at the same rate. Given the reliability with which the landmark and the corner of the pool could be used by rats to predict the location of the platform was equal, it is likely that the two cues were equally salient.

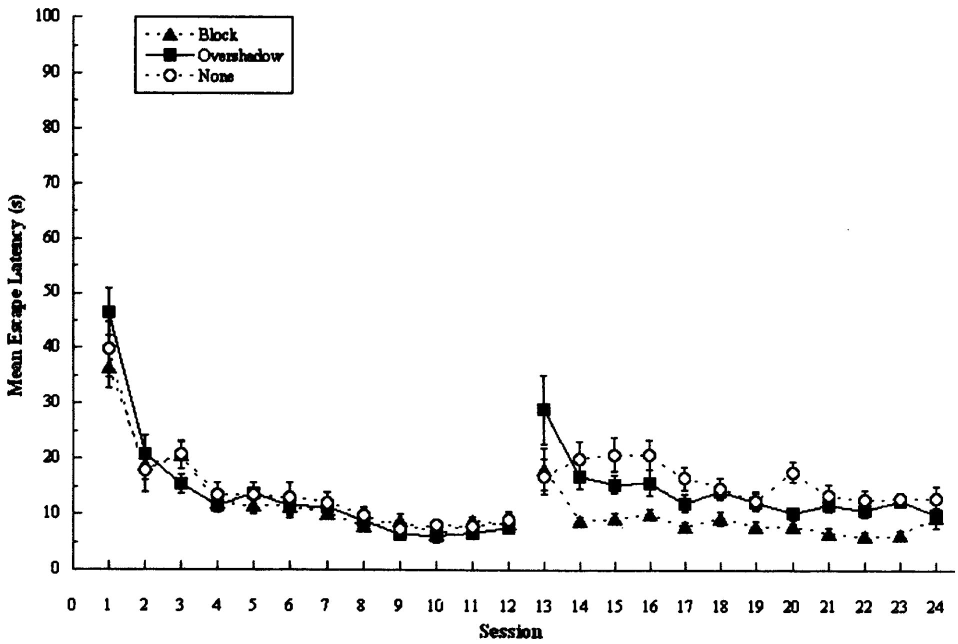


Figure 2.06. Mean escape latencies for the groups during training with the rectangular pool in Stage 1 (left-hand side) and with triangular-shaped pool (right-hand side) during Stage 2 (error bars represent ±1 standard error of the mean).

Following acquisition trials that took place in the rectangular pool all further training was conducted in a triangular-shaped pool and the group's mean escape latencies for this stage of the experiment are illustrated in figure 2.06 (right-hand side). In general, Group Block found the platform more quickly during Stage 2 than the other two groups. Group None took the longest time to find the platform. Nevertheless all groups showed small decreases in their escape latencies over the final 12 sessions and a mixed two-way ANOVA of escape latencies for the three groups during the final 12 sessions showed significant main effects of session, F(11, 286)= 7.04, Mse= 49.70, p= 0.00, η_p^2=0.21, and of group, F(2, 26)= 4.75, Mse= 208.25, p=0.018, η_p^2=0.27, but the interaction of Group x Session, F(22, 286)= 1.37, Mse= 49.70, p=0.128, η_p^2=0.10, was not significant. Tests of simple main effects showed that Group None was significantly slower to find the platform than Group Block (F(1, 26)= 8.98, Mse= 208.25, p= 0.01, η_p^2=0.26). Despite appearances the difference between Group None and Group Overshadow failed to reach significance when the critical value of F was corrected using the Sheffé procedure F(1, 26)= 5.31, Mse= 208.25, p= 0.03, η_p^2=

0.17. There was no significant difference between the Groups Overshadow and Block $\underline{F}(1, 26)= 0.48$, Mse= 208.25, $\underline{p}= 0.50$, $\eta_p^2=0.02$. For the latter comparison the critical value of F was corrected using the Sheffé procedure. It is not surprising the performance of Group None was inferior compared to that of the other two groups. The only cue they had for finding the platform was the shape of the pool, whereas Groups Block and Overshadow could refer to either the shape of the pool or the landmark. Presumably rats found it easier to identify the location of the platform when two rather than one cue was available for locating it. It is likely, for example, that two cues specified the whereabouts of the platform more precisely than just one cue.

The group mean percentages of trials on which rats went directly to a corner containing a platform after being released into the rectangular pool are illustrated for the three groups during Stage 1 of the experiment in figure 2.07 (left-hand side). From the outset rats of Groups None and Block, for which the platforms could be found by referring to the landmarks, swam directly to a corner with a platform on a greater percentage of trials than rats of Group Overshadow, for which the platforms could be found by referring to the shape of the pool. This difference among the groups had largely disappeared by the end of training, at which point all three groups were swimming directly to a corner containing a platform on over 60% of trials.

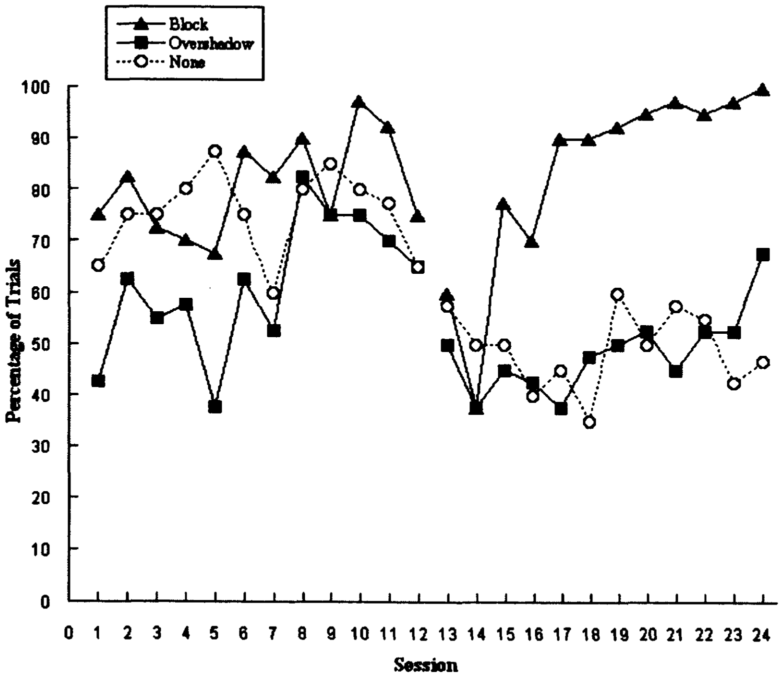


Figure 2.07. Mean percentages of trials the groups entered first the correct corners of the rectangular (left-hand column) and triangular-shaped pools (right-hand column) respectively.

To compare the performance of the groups, the mean percentages of trials on which individual subjects swam directly to a corner with a platform, were calculated for the 12 sessions combined. A comparison of these means, using the Mann-Whitney U test, revealed that Group Overshadow swam directly to a correct corner of the rectangle significantly less often than either Group Block U(10, 10)=2, or Group None U(10, 9)=2. The difference between the last two groups was not significant, U(10, 9)=33. At first sight there seems to be no obvious reason why Groups Block and None should have swum to a corner occupied by a platform significantly more often than Group Overshadow. However, it is possible that the landmarks had some unconditioned property that encouraged rats to approach them. Such behaviour would be of great benefit to Groups Block and None because each platform was always located in the vicinity of a landmark. However, the two platforms were only intermittently positioned near a landmark for Group Overshadow. Thus, the unconditioned property that encouraged this group to approach the landmark would interfere with escape from the pool on half the trials. Nonetheless all subjects in each group swam directly to a corner containing a platform on the majority of trials during Stage 1 of the experiment, which confirms that each group was able to discriminate accurately between the corners containing the platforms and the remaining incorrect corners of the pool.

The group mean percentages of trials on which rats went directly to a corner containing a platform after being released into the triangular pool during the Stage 2 are also depicted in figure 2.07 (right-hand side). It is apparent that pre-training Group Block to locate the platforms by referring to the landmarks in Stage 1 enabled this group to find the platform rapidly during the second stage. In the case of the remaining groups, however, the absence of the landmark for Group None, or the presence of the landmark, which had previously been irrelevant for Group Overshadow, resulted in less accurate performance than by the experimental group.

To compare the performance of the groups, the mean percentages of trials on which individual subjects swam directly to a corner with a platform were calculated for the 12 sessions combined. A comparison of these means showed that the performance of Group Block was superior to that of Group None, $\underline{U}(10, 9)=0$, and that of Group Overshadow, $\underline{U}(10, 10)=0$. The latter groups did not differ, $\underline{U}$ (10, 9)=35. These results confirm the general observations made above: that pre-training Group Block with the landmark in Stage 1 enabled rats to identify speedily the location of the platform during Stage 2. One inference that can be made from this result is that the landmark was an effective cue for finding the platform not only in the first, but also in the second stage of the experiment for the blocking group.

To determine if the groups were able to discriminate the corner containing the platform from the other two corners of the pool, for each subject the mean percentage of trials they swam to a particular corner for the 12 sessions combined was calculated. For the correct corner, the other corner at the base of the triangle, and the apex, respectively, these percentages were: 86, 6.5, and 7.5 for Group Block; 48.3, 26.0 and 25.7, for Group Overshadow and; 51.0, 19.3, and 29.7 for Group None. Paired comparisons revealed that the correct corner was entered first significantly more often than the other corner at the base of the triangle, or the apex for Group Block, Ts(10)=0, Group Overshadow, Ts (10)<7, and Group None, Ts(9)< 4. These results indicate that all rats, regardless of their group, discriminated the corner with the platform from the other two corners of the pool. For the purposes of analysing the results from the test session in the triangular pool, it was divided into four quadrants of unequal area (see figure 2.05, right-hand column). The quadrants were created by dividing first the pool into two equal halves with a line that passed through the apex of the triangle. Each half was then further divided into two with a line that was perpendicular to the line just described and passed through the midpoint of the triangle which was coincident with the midpoint of the circular pool. The two quadrants at the base of the triangle were thus of equal size and substantially larger than the quadrants at the top of the triangle. The correct quadrant was that previously occupied by the platform and the incorrect quadrant was directly opposite the one just described.

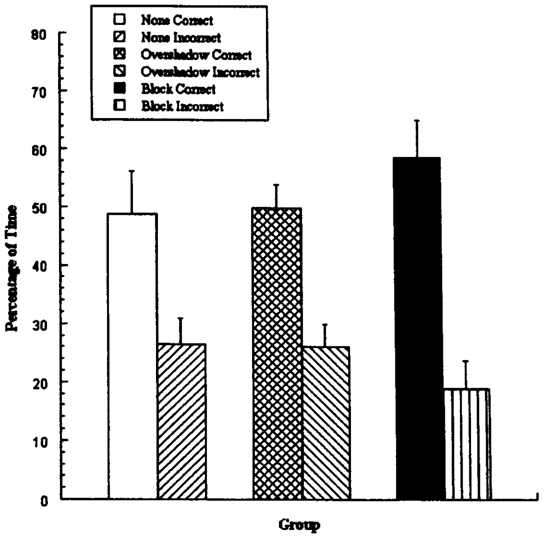


Figure 2.08. Mean percentages of time the groups spent searching in the correct and incorrect quadrants of the triangular-shaped pool during the test without either the platform or the landmark (error bars indicate ±1 standard error).

The mean percentages of time spent in the correct and incorrect quadrants of the pool during the full 60 seconds of the test trial are shown figure 2.08. All three groups showed a preference for searching in the correct rather than the incorrect quadrant, and there is an indication that this preference was strongest in the blocking group. A two-way ANOVA for the three groups and of time spent in the correct and incorrect quadrants, showed a significant main effect of quadrant, $\underline{F}(1, 26)=50.39$, Mse= 239.64, $\underline{p}=0.00$, $\eta_p^2= 0.66$, but neither the interaction of Group x Quadrant, $\underline{F}(2, 26)=1.76$, Mse= 239.64, $\underline{p}= 0.19$, $\eta_p^2= 0.12$, nor the main effect of group, $\underline{F}(2, 26)= 0.95$, Mse= 74.65, $\underline{p}= 0.95$, $\eta_p^2= 0.00$, were significant.

These findings confirm that all three groups during Stage 2 acquired a preference for the quadrant of the triangular pool containing the platform. Importantly this preference was not affected by the presence of the landmark for Group Block even though it had previously served as a reliable cue for finding the platform. Moreover, there was no indication that the preference for swimming in the correct quadrant exhibited by Group Overshadow was influenced by the presence of the landmark in the second stage. There was no hint in this experiment that the landmark in either the blocking or the overshadowing group interfered with learning about the position of the platform with reference to the triangular shape of the pool.

The results depicted in figure 2.07 (left-hand column), make it extremely clear that the blocking group learned to use the landmark to find the platform during Stage 1 and learned quickly to use it again during Stage 2 for the same purpose. Together these findings suggest first, that the failure to find blocking was not because the landmark failed to act as an effective cue for finding the platform. Second, it is also unlikely blocking failed simply because subjects failed to notice the landmark during training with the rectangular or triangular pool shaped pools.

Moreover, according to theories of learning (Rescorla & Wagner, 1972) because landmark control was substantially greater in the blocking group than for the other two groups during Stage 2, this makes it extremely likely that blocking should have occurred. Clearly it did not. In addition the results of the test trial for the blocking group also had the potential for showing a blocking effect. If blocking had occurred this group would have spent an equal proportion of time searching in the correct and incorrect quadrants of the pool during the test. Clearly, they did not. Instead despite extensive pre-training with the landmark in first stage, and its continued presence during the second stage, Group Block showed a substantial preference for searching in the correct region of the pool. Hence, the results of the training and test stages of the experiment show for Group Block, a failure to reveal the effects of blocking.

Compared to the blocking group Groups None and Overshadow showed only a weak preference for searching the corner of the triangular-shaped pool containing the platform, which implies they learned rather little about the geometry of the pool in the second stage. Consequently, it could be argued that these groups provide poor control against which to assess the effects that pre-training with the landmark had on the blocking group. It is worth bearing in mind however, that Group None swam to the correct corner on over 50% of trials in Stage 2 as did Group Overshadow, making their performances in the triangular-shaped pool above that expected by chance.

Together the results of Experiment 2 lend considerable support to the idea that there is something special about spatial learning based on the shape of an environment (for example, Cheng, 1986; Gallistel, 1990). They show further that learning based on the shape of an environment can occur in the absence of landmarks, but more importantly that the presence of landmarks do not influence such learning. In addition the failure to detect the effects of cue competition here is more compelling than the failure found in Experiment 1, because this experiment utilised a blocking rather than an overshadowing design.

2.03. Experiment 3

The results of the previous experiment showed unequivocally that despite pre-training with the landmark during Stage 1 and its continued presence during Stage 2, the blocking group exhibited a strong preference for swimming in the correct quadrant of the triangular pool during the test. In short, the landmark failed to block learning based on the shape of the triangular pool. In that experiment pre-training took place in a rectangular pool whilst further conditioning and testing took place in the

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triangular-shaped pool. Experiment 3 was conceptually identical to Experiment 2, except that rats were trained first to escape from a triangular-shaped pool before being trained and tested in a rectangular pool (see figure 2.11).

During Stage 1, three groups of rats were required to find a single submerged platform that was located in one corner at the base of the triangular pool (see figure 2.09). The platform always occupied the same corner for Groups Overshadow and None, but for Group Block the platform was moved randomly between the two corners at the base of the triangle. A single landmark was always placed near the platform for Group Block. However, for the two remaining groups the landmark was moved between the two corners at the base of the triangle. Thus, for Groups Overshadow and None the landmark and platform were located in the same corner for half of the trials, whilst for the remaining trials they occupied different corners at the base of the triangle.

As a consequence of training the blocking group in the manner described, the landmark but not the corners of the pool could be used by rats to predict accurately the location of the platform. For the other two groups, this situation was reversed: the corner of the triangular pool, but not the landmark could be used to predict accurately the location of the platform.

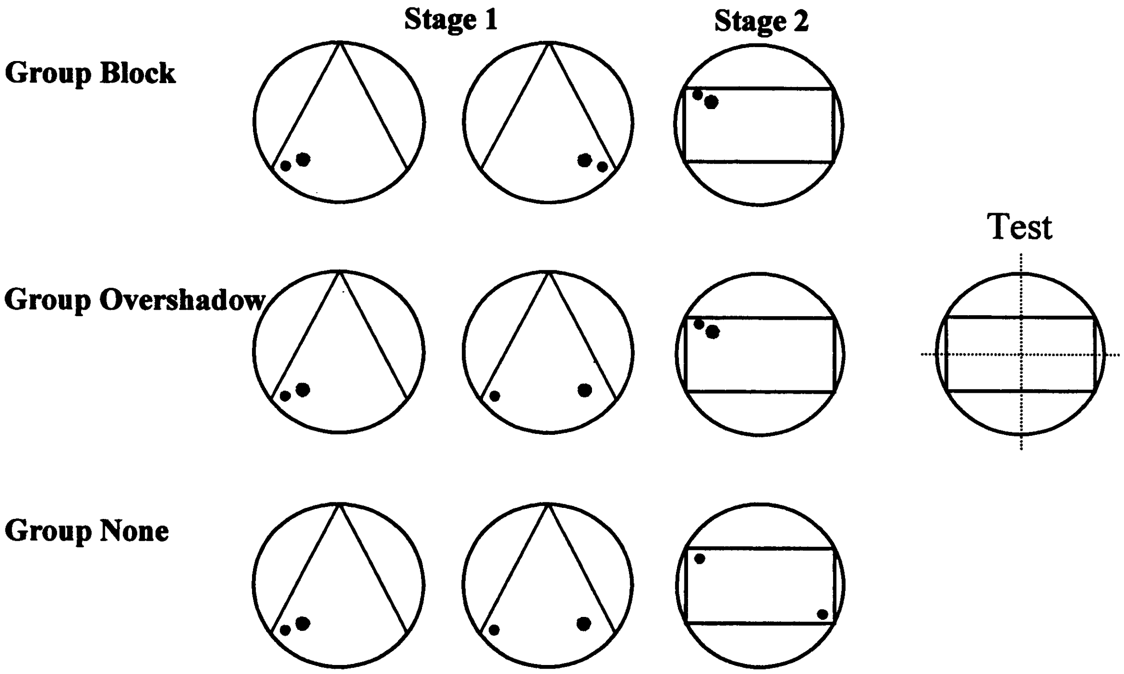

Figure 2.09. The design and apparatus used for experiment 3. Pre-training with the landmark took place in the triangular-shaped pool (left-hand column) and further conditioning during Stage 2 was carried out in the rectangular pool (right-hand column). Filled black circles show the location of the platform and shaded circles the landmark. The test was conducted in the rectangular pool without any objects in it (extreme right-hand column).

During Stage 2 of the experiment Groups Block and Overshadow were treated identically and were required to escape onto a submerged platform located in one corner of a rectangular shaped pool, where a landmark was also situated. By comparison, Group None was trained in the absence of the landmark. Instead two platforms occupied geometrically equivalent corners of the pool. Finally, rats received a single test trial that was conducted without either the landmark or the platform(s). The test was identical to the one undertaken at the end of Experiment 1 and the time rats spent searching in the quadrant previously occupied by the platform and the geometrically equivalent quadrant was recorded. If pre-training with the landmark should block learning about the position of the platform with reference to the shape of the pool during Stage 2, then the blocking group should not exhibit a preference for the correct quadrants of the pool during the test trial. On the other hand, the results from the previous experiment lead to the prediction that during the test all three groups should demonstrate a similar preference for the correct quadrants.

Method

Subjects and apparatus The 30 rats were from the same stock, of similar experience, and housed in the same conditions as Experiment 1. At the start of the experiment they were assigned at random in equal number to the three groups. The apparatus was identical to that used in the previous experiment and comprised the rectangular pool, the triangular pool, the platform and the landmark.

Procedure In each of the 12 sessions of Stage 1, rats from each group were required to escape from the pool by swimming to the submerged platform. For half the rats in Groups None and Overshadow the platform occupied the corner at the left-hand end of the curved wall of the triangular pool, and for the remaining rats the corner at the right-hand end of the curved wall was used. For Group Block the platform occupied both of these locations equally often in each session according to a random sequence. The landmark was always near the platform for Group Block, but for the other groups it was moved randomly between the two corners at the base of the triangle according to the same sequence that determined the position of the landmark, and platform, for Group Block. The centre of the landmark was always 30 cm from the corner of the pool, on an imaginary line that bisected the two corners at the base of the triangular pool. The centre of the landmark was always 60 cm from the corner on the same imaginary line.

In each of the 12 sessions during Stage 2 of the experiment Groups Block and Overshadow were treated identically and were trained to find a single submerged platform, with reference to a landmark nearby. For these groups the platform in addition to the landmark was located in one of two geometrically equivalent corners of the rectangular pool. Together the platform and landmark occupied each geometrically equivalent corner twice in each session and was moved between these positions in a random sequence. For Group None two platforms were present during training and occupied geometrically equivalent corners of the pool. For half the rats in each group the platform occupied the corners with the short wall to the left of the long wall and for the remaining rats it occupied the corners with the reverse geometric properties. The centre of the platform(s) was 30 cm from the corner of the rectangle, on an imaginary line that bisected geometrically equivalent corners of pool. The landmark was located on the same imaginary line, 60 cm from the corner containing the platform, for the blocking and overshadowing groups but it was never present for the control group.

The final trial of the final session was a test trial conducted without the platform or the landmark. For the test rats were released from the centre of the pool and allowed to swim freely for 60 s. For the purpose of the test the pool was divided into four quadrants of equal area (see Figure, 2.09) and the time rats spent in the quadrant previously occupied by the platform and the one geometrically equivalent to it was recorded. Procedural details relating to the test that have been omitted were the same as for Experiment 1.

Results and Discussion

The groups' mean escape latencies for acquisition trials that took place in the triangular pool over the first 12 sessions of the experiment can be seen in figure 2.10 (left-hand side). Generally all groups showed a decrease in their escape latencies. A mixed two-way ANOVA of escape latencies over the 12 sessions for the three groups showed a main effect of session, F(11, 297)= 129.26, Mse= 71.57, p= 0.00, η_p^2= 0.83, a significant interaction of Group x Session, F(22, 297)= 2.07, Mse= 71.57, p=0.00, η_p^2= 0.13, but the main effect of group was not significant, F(2, 27)=0.74, Mse=185.25, p=0.49, η_p^2=0.05. Tests of simple effects showed that the effect of session for each group was significant and these results were: F(11, 297)=38.94, Mse= 71.57, p= 0.00, η_p^2= 0.59, for Group None; F(11, 297)= 35.07, Mse= 71.57, p= 0.00, η_p^2=0.57, for Group Overshadow; and F(11, 297)=59.41, Mse= 71.57, p=0.00, η_p^2= 0.69, for Group Block. Additional tests of simple effects showed that Group Block was slower to find the platform than Groups Overshadow (F(1, 324)=7.48, Mse= 75.40, p=0.00, η_p^2= 0.02) and None (F(1, 324)=12.31, Mse= 75.40, p=0.00, η_p^2= 0.04). No other comparisons, when the critical value of F was adjusted using the Sheffé procedure were found to be significant. The interaction between Group x Session can thus be accounted for by performance differences between the groups during the first session.

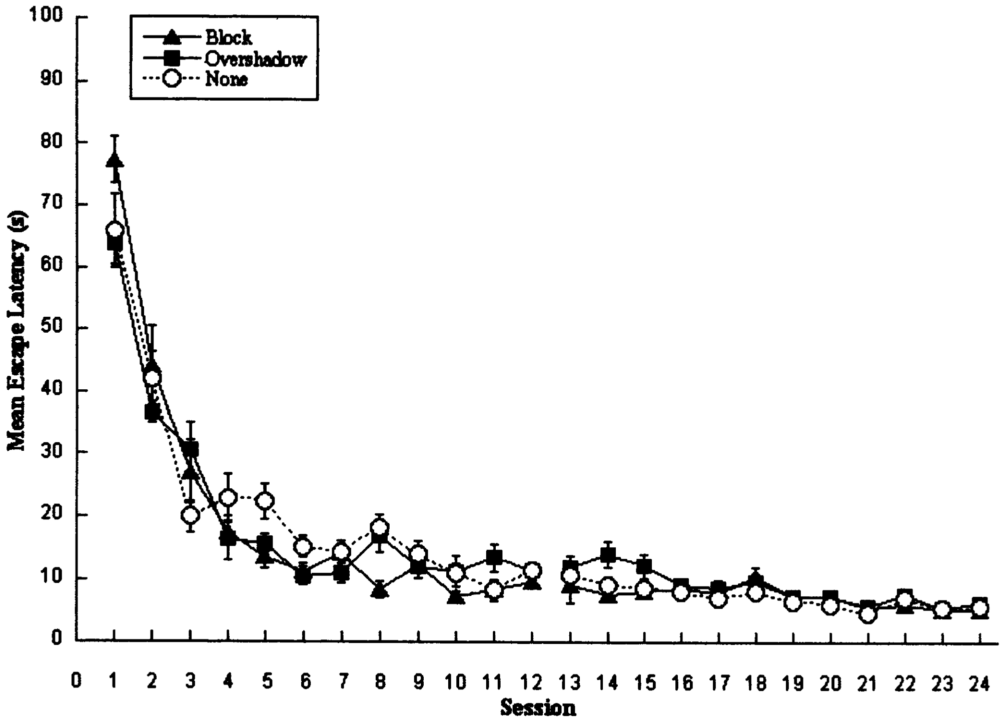

Figure 2.10. Mean escape latencies for the groups during training with the triangular-shaped pool in Stage 1(left-hand side) and with the rectangular pool (right-hand side) during Stage 2 of Experiment 3 (error bars show ±1 standard error).

During the final session of training with the triangular-shaped pool all three groups were at similar performance levels. One implication of this result is that the shape of the pool for Groups None and Overshadow were just as effective for finding the platform as the landmark was for Group Block.

The group's mean escape latencies for Stage 2 of the experiment are depicted in figure 2.10 (right-hand side). In general all groups showed a small decrease in their escape latencies over the final 12 sessions. There were no apparent differences between the groups, except during the second and third sessions of training where Group Overshadow appeared to be slower at escaping from the pool than the other two groups. A mixed two-way ANOVA of escape latencies over the 12 sessions showed significant main effects of session, F(11, 297)= 9.40, Mse= 11.40, p= 0.00, η_p^2= 0.15, and of group, F(2, 27)=3.81, Mse= 23.10, p= 0.04, η_p^2= 0.22 but the interaction of Group x Session was not significant, F(22, 297)= 1.10, Mse= 11.40, p= 0.35, η_p^2= 0.04. When the critical value of F was corrected using the Sheffé procedure, over all of the sessions combined, Groups Block and None did not differ, F (1, 27)= 0.02, Mse= 23.10, p= 0.90, η_p^2= 0.00. Moreover the difference between Group Overshadow and each of Groups Block (F(1, 27)=5.39, Mse= 23.10, p=0.03, η_p^2= 0.17) and None (F(1, 27)=6.00, Mse=23.10, p=0.02, η_p^2= 0.18) also failed to reach significance using the same criteria as that used for the previous calculation.

At the outset of Stage 2, Group Block found the platform with some ease. One interpretation of this result is that rats found the platform by referring to the landmark, a strategy that was effective for escaping from the triangular-shaped pool during the first stage. Compared to the overshadowing group, Group None also took very little time to find the platform during Stage 2. One simple explanation for their superior performance is that they were trained with two platforms rather than one, which made is easier to escape from the pool.

The mean percentages of trials on which subjects swam directly to the correct corner: that containing the platform, in the triangular-shaped pool during the first stage of training is shown for the three groups in the left-hand side of figure 2.11. Training was more successful with Group Block for which the landmark was relevant for finding the platform than for the other two groups for which the shape of the pool was relevant for finding the platform. Comparisons of individual mean percentages of trials on which the correct corner was entered first for the 12 sessions combined revealed a significant difference between Group Block and each of Groups None and

Overshadow, Us(10, 10)<8, but the difference between the latter two groups was not significant, U(10, 10)=28. One interpretation of these results is that the landmark, for the blocking group, was a more effective cue for finding the platform than the corner of the triangular pool was for the other two groups. And one reason that rats were able to use the landmark more effectively than the shape of the pool for finding the platform is because the saliency of the landmark may have been greater than that of the triangular-shaped pool.

The mean percentages of trials in the triangular arena on which the correct corner, the opposite corner and the apex, respectively, were entered first for the 12 sessions combined were: 72, 17 and 21 for Group Block; 56, 25, and 19 for Group Overshadow; and 49, 31, and 20 for Group None. Paired comparisons revealed that for each group the correct corner was entered first significantly more often than either the opposite corner or the apex, Ts(10)<2. These findings confirm that each group was able to discriminate between the correct corner and the other two corners of the triangular-shaped pool. Thus, Groups Overshadow and None were able to use the corners of the triangular pool sufficiently well to find the platform and Group Block was able to identify the position of the platform by referring to the landmark.

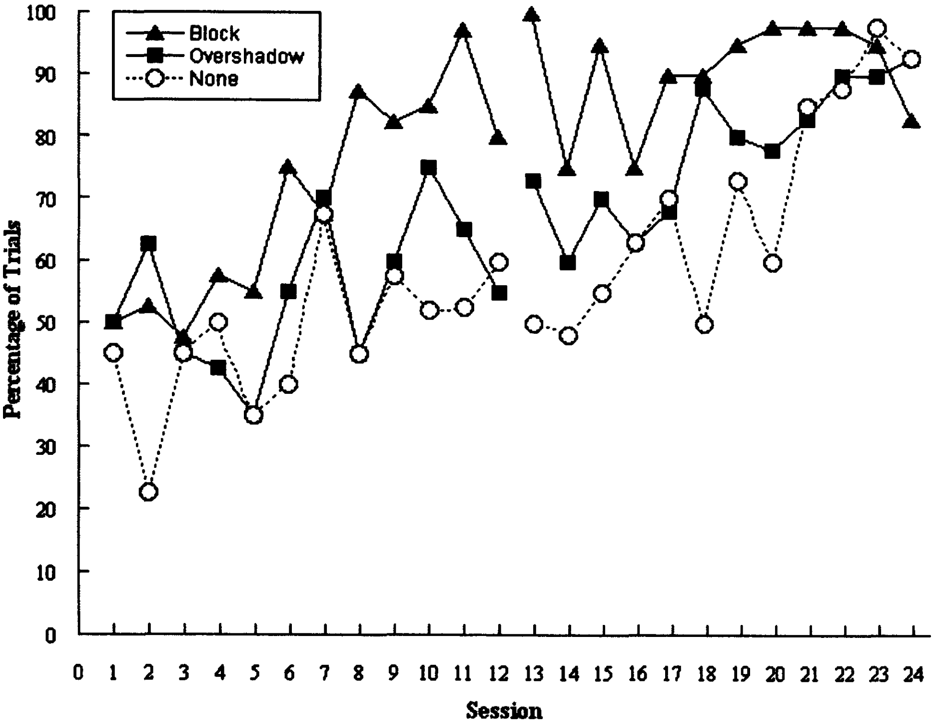

Figure 2.11. Mean percentages of trials the groups entered first the correct corner of the triangular-shaped pool during Stage 1(left-hand side) and the equivalent corner of the rectangular pool during Stage 2 (right-hand side).

The mean percentages of trials on which the groups swam to a geometrically correct corner: the one containing the platform and its geometric equivalent; are shown for each session of Stage 2 in the right-hand column of figure 2.11. Initially, Group Block swam directly to a geometrically correct corner on a greater proportion of trials than the other two groups, but by the end of the experiment all of the groups were expressing a similarly strong preference for swimming directly to a geometrically correct corner. Comparisons of individual mean percentages of trials on which a geometrically correct corner was entered first for the 12 sessions combined revealed a significant difference between Group Block and each of the other two groups, Us(10, 10)=0, which did not differ, U(10, 10)=27. Moreover, every subject swam to a geometrically correct corner on more than half of the trials.

The above results make clear that at the outset of Stage 2 Group Block swam to a geometrically correct corner more often than the other two groups. In fact, Group Block swam predominantly to the corner with the platform rather than to the geometrically equivalent corner. Searching, at least at the beginning of Stage 2, must have therefore been under the control of the landmark, which implies it had become an effective cue for finding the platform during Stage 1.

Importantly, every subject approached either the corner containing the platform or its geometric equivalent on more than half of the trials. The ability of rats to find the platform was therefore above that expected by chance. For this reason it could be argued that each cue, the landmark and shape of the rectangular pool, was effective for finding the platform.

The mean percentages of time the groups spent searching in the correct quadrants of rectangular pool during the 60-s test trial are illustrated in figure 2.12. One sample t-tests revealed that all groups spent significantly more than half of their time searching in the corner previously occupied by the platform and its geometrically equivalent corner. These results were: $\underline{t}(9)= 3.71$, $p= 0.00$, for Group None; $\underline{t}(9)= 2.65$, $p=0.01$, for Group Overshadow; and $\underline{t}\ (9)= 3.24$, $p= 0.01$, for Group Block. Figure 2.14 shows a lack of apparent between group differences and a one-way ANOVA of time spent in the correct quadrants showed that the differences between the groups were not significant, $\underline{F}\ (2, 27)= 0.44$, Mse= 45.98, $\underline{p}=0.65$, $\eta_p^2=0.03$.

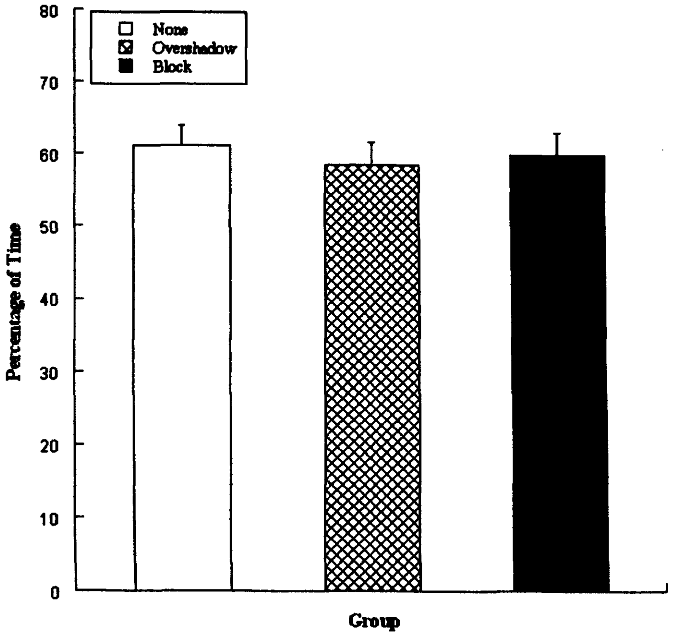

Figure 2.12. Mean percentages of time the groups spent searching in the correct quadrants of the rectangular pool during test without the platform and landmark (error bars represent ±1 standard error of the mean).

Given that all three groups acquired only a modest preference for searching the correct quadrants of the pool it could be argued that the test trial was relatively insensitive to detect the effects of cue competition. Had cue competition been successful, however, then blocking and overshadowing groups would have spent less than half of their time searching the correct quadrants of the pool. In contrast, every group spent more time than that expected by chance searching the correct quadrants of the pool which implies cue competition failed.

The results of the test trial for Experiment 3 are similar to the equivalent results of Experiment 2 and confirm that all three groups acquired a significant preference for searching the correct quadrants of the rectangular pool. This preference was not affected by pre-training with the landmark in the blocking group, or by its presence during the second stage for the overshadowing group. Thus, like the results of the previous experiment there was no indication that the landmark in either the blocking or overshadowing groups influenced, to any degree, learning based on the shape of rectangular pool.

Together the results of Experiments 2 and 3 provide substantial evidence in support of the idea that pre-training with the landmark failed to block learning based on the triangular or rectangular shaped pools. These results, as well as the failures to find overshadowing in any of the previous experiments, lend a great deal of support to the idea that animals possess a Geometric Module which is, for the most part, impervious to the influence of landmarks (Cheng, 1986; Gallistel, 1990).

The results also suggest that spatial learning based on the shape of an environment cannot be explained adequately by associative learning theory (Rescorla & Wagner, 1972). However it might be possible for associative learning theory to explain the absences of cue competition reported here, by assuming that the landmark was of relatively low salience compared to that of the triangular and rectangular shaped pools. Pavlovian conditioning experiments have shown, for example, that blocking will be ineffective if the pre-trained stimulus is less salient than the added stimulus. One experiment which illustrates this principle was conducted by Hall, Mackintosh, Goodall and del Martello (1977) who used a weak stimulus to signal a reinforcer before it was presented in compound with a stronger stimulus and paired with the same reinforcer. Subsequent test trials with the strong stimulus revealed very little evidence of blocking. Moreover, as Hall et al (1977) point out this finding can be accommodated by several different theories of associative learning (Mackintosh, 1975, Rescorla & Wagner, 1972). If it were the case therefore, that the landmark in these experiments was of low salience compared to the shapes of the pools then not only would the results be compatible with studies of Pavlovian conditioning, but they could also be explained by theories of associative learning that predict that cues compete for the control they acquire over behaviour (Rescorla & Wagner, 1972). Fortunately the results of Experiments 2 and 3 can be used to assess the saliency of the landmark, compared to that of the triangular and rectangular pools. However, as will become clear, the idea that cue-competition failed as a result of the relatively low salience of the landmark deserves little merit.

First, consider the initial sessions of training in Experiment 2, during which rats were required to escape from a rectangular pool by finding one of two platforms that were located in geometrically equivalent corners of the pool. There were also two landmarks in the pool, which were also placed in geometrically equivalent corners. For the blocking group the corners containing the platform varied randomly for each trial, but the landmarks were always placed near the platforms. By comparison, for the overshadowing group the platforms remained in the same corners of the rectangle, whilst the landmarks were moved between geometrically equivalent corners of the pool and in the same manner as the blocking group. Thus, the blocking group could use the landmarks, but not the corners of the pool to predict accurately the location of the platforms. For the overshadowing group this situation was reversed: they could use the corners of the pool, but not the landmark to predict accurately the location of the platforms. As such, the reliability with which Group Block could use the landmarks to find the platform was identical to the reliability with which Group Overshadow could use the corners of the pool to find the platform. This is important because the reliability with which cues can be used to predict the occurrence of a US has been shown to influence the rate of conditioning (Rescorla, 1986). Thus any differences between the rates at which these groups learned to locate the platform must have been a result of some other factor.

According to the Rescorla-Wagner model (1972) one factor that can dramatically influence the rate of conditioning is stimulus salience and this model predicts that asymptotic performance is reached more rapidly with salient rather than weak stimuli. It follows then, that if the salience of the landmark was substantially weaker than that of the shape of the rectangular pool, Group Block should have been less accurate than the overshadowing group at identifying a corner occupied by the platform. Figure 2.07 shows the opposite result, implying that the salience of the landmark was greater than that of the rectangular shaped pool. Given this finding it is difficult to argue that the failure to find blocking in Experiment 3 was a consequence of the low salience of the landmark compared to that of rectangular pool used during the second stage of that experiment. Similarly it is also difficult to argue that the failure to find overshadowing in Experiment 1, was a result of the low salience of the landmark compared to that of the rectangular pool used in that experiment.

The initial period of training for Experiment 3 can also be used to assess the salience of the landmark relative to the shape of the triangular-shaped pool (see figure 2.11, left-hand side). In that experiment rats were required to find a submerged platform located in one corner at the base of a triangular-shaped pool. For the blocking group a landmark was positioned near to the platform and was moved with it, in a random sequence, from one corner at the base of the triangular pool to the other corner at the triangle's base. For the overshadowing group the platform remained stationary in one corner at the base of the triangle, whilst the landmark was moved between the two corners at the base of the triangle, in a random sequence. As a result of training the groups in this way, the reliability with which Group Block could use the landmark to locate the platform was identical to that of the corners of the pool for Group Overshadow. Hence, any difference between the groups, in the rate they learned to locate the platform, would have been influenced by some factor other than by the reliability with which the landmark or the shape of the pool could be used to find the platform.

As with Experiment 2, the results of Stage 1 for Experiment 3 show unequivocally that Group Block were more consistent than the overshadowing group, at swimming directly to a corner occupied by the platform (see figure 2.11). The implications of this finding should now be clear: the salience of the landmark must have been greater than that of the triangular-shaped pool. For this reason it would be unreasonable to attribute the failure to find blocking in Experiment 2 to the landmark being less salient than the shape of the triangular-shaped pool used during Stage 2 of that experiment.

To reiterate, the results from Stage 1 of Experiment 2 show that the landmark was more salient than the rectangular pool, whilst the results of the equivalent stage for Experiment 3 show that the landmark was more salient than the triangular-shaped pool. It is thus highly unlikely that cue competition failed in any of the previous experiments as a result of the landmark being less salient than the shape of either the rectangular or triangular pools. Traditional theories of associative learning (Rescorla & Wagner, 972) predict the landmark, under the conditions described, should have acquired sufficient control over searching for the platform to restrict learning based on the geometric properties of the arenas used. Associative learning theories, then, fall somewhat short in their explanation for the effects that I have described.

2.04. Experiment 4

The results of Experiments 2 and 3 provided evidence to suggest that the landmark was more salient than the shape of the triangular and rectangular pools. It is therefore unlikely that cue competition failed in those studies due to the relatively low salience of the landmark. The current experiment was designed primarily to extend the generality of results found in the previous two studies by using a different type of rectangular arena. If the previous findings can be shown to be both reliable and general, then it would strengthen considerably the conclusions that can be drawn from them.

As a step toward achieving these goals the experiment took place in a circular pool. Instead of using the four boards to create the rectangular shape, four cylinders were attached vertically to the walls of the pool at points where the corners of the rectangular arena would normally be. These cylinders thus created a virtual rectangle which had the same dimensions as the rectangle used for previous experiments (see figure 2.13). Learning based on the shape provided by the landmark array would be revealed if subjects searched in geometrically equivalent corners of the rectangle. Moreover, it was expected that removing the walls of the rectangle would serve to reduce its salience, compared to the enclosed rectangular arena used for the previous studies. By reducing the salience of the shape described by the test arena in this way, it is conceivable that the presence of a landmark near the platform during the training trials will prevent the shape created by the four cylinders gaining control over searching for the platform. Put simply, the landmark might be expected to overshadow learning based on the shape of the array.

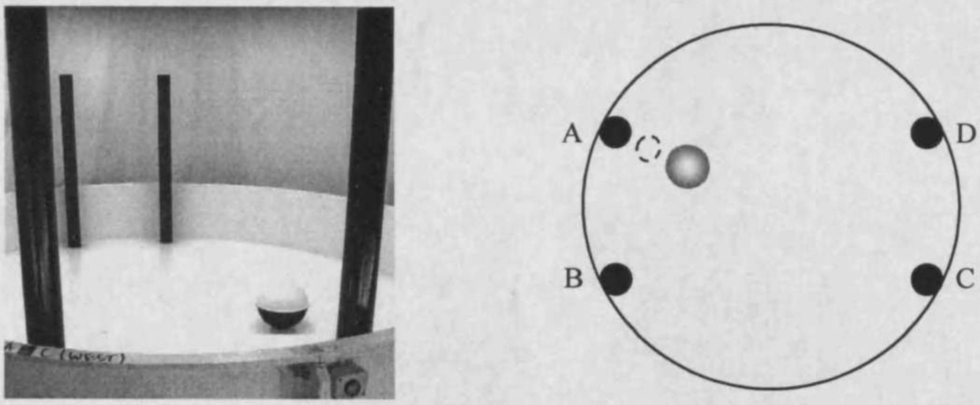

Figure 2.13. The apparatus used for Experiment 4. Although the perspective distorts the image somewhat the image on the left shows the four black cylinders and the rectangle measuring 1.8 m x 0.9 m they describe. The landmark is located near right-hand corner of the array. The landmark is not drawn to scale. In the plan view of the apparatus shown on the right-hand side, the four cylinders are given by the black filled circles, the platform by the dashed line and the landmark by the grey filled circle. The letters A, B, C and D have been used label the corners of the rectangle.
Two groups were used to test the above prediction.

Each group was trained to escape onto a submerged platform located in one corner of the rectangle described by the four cylinders. For Group Landmark, but not Group None, the same landmark used for Experiment 1 was placed near the platform.

Method

Subjects and apparatus The 20 rats were from the same stock, housed in the same manner, and of similar experience to those used for pervious experiments. The experiment was conducted in the circular pool and with the same spherical landmark and platform that was described for Experiment 1. A virtual rectangular shape, 1.8 m x 0.9 m, was created by attaching four cylinders vertically to the sides of the pool at points that corresponded to the corners of the rectangle used in Experiment 1. The cylinders were constructed from black plastic tubing with an external diameter of 6.8 cm. When placed in the pool, the cylinders extended to a height of 90 cm above the surface of the water (see figure 2.13).

Procedure In each of the first 11 sessions of training both groups were required to escape from the pool by swimming to the platform. For both groups the platform was located in one corner of the rectangular area that was defined by the four cylinders. The centre of the platform was 30 cm from the nearest edge of the nearest cylinder directly above an imaginary line that bisected the corners of the rectangle. The centre of the spherical landmark, which was used for Group Landmark only, was situated on the same line as the platform with its centre 30 cm from the centre of the platform. Rats were lowered into the water facing the wall of the pool at the four points that were half way between adjacent cylinders. Each release point was used once in a random sequence in every session.

The first three trials of Session 12, the test session, were conducted in the same manner as for the previous stage. For the final trial there were no objects in the pool apart from the cylinders. Rats were released from the centre of the pool, their orientation, in relation to the rectangular array, was varied randomly for each subject. They remained in the pool for 60 s. The curtains were drawn around the pool throughout the experiment and the orientation of the rectangle was changed randomly from trial to trial. Procedural details that have been omitted were the same as for Experiment 1.

The method of recording the behaviour of subjects was based on that used for Experiment 1 but with two changes. First, during the training trials the segments of the circles, which were used to identify the corner rats approached first, extended beyond the boundary of the virtual rectangular area to the edge of the pool. An entry into a corner was deemed to have taken place when a subject's snout entered a segment of a circle with a radius of 40 cm whose centre was located at the centre of each cylinder. Second, for the test trial the regions of the pool that were used to define the correct and incorrect quadrants of the virtual rectangular arena were extended beyond the boundary of the rectangle to include the remainder of the pool. Thus the correct and incorrect quadrants in the following section refer to four equal quarter-segments of the circular pool, rather than to four equal regions of the rectangular arena.

Results and Discussion

The mean escape latencies for the groups during the training trials of each session of the experiment can be seen in figure 2.14. The latencies for both groups decreased as training progressed, but throughout the experiment they were consistently shorter for Group Landmark than Group None. A two-way ANOVA of individual mean escape latencies for each of the 12 sessions revealed a significant effects of group, $\underline{F}(1, 18)= 52.80$, Mse= 437.41, $\underline{p}= 0.00$, $\eta_p^2= 0.75$, and of session, $\underline{F}(11, 198)=44.62$, Mse= 139.73, $\underline{p}=0.00$, $\eta_p^2= 0.71$, but the interaction Group x Session was not significant, $\underline{F}(11, 198)=1.11$, Mse= 139.733, $\underline{p}=0.35$, $\eta_p^2=0.06$.

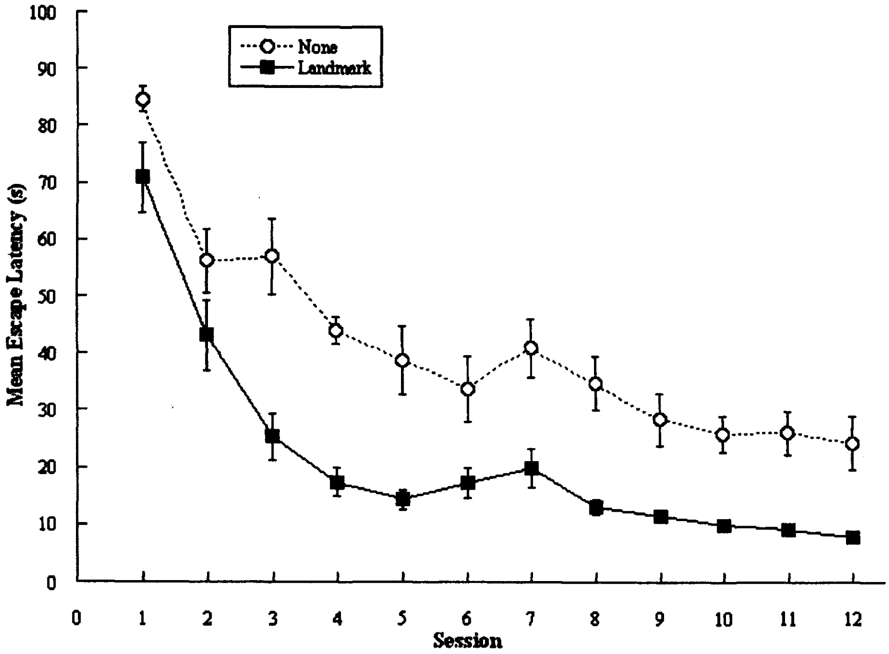

Figure 2.14. Mean escape latencies for the groups during the acquisition stage of Experiment 4 (error bars represent ±1standard error).

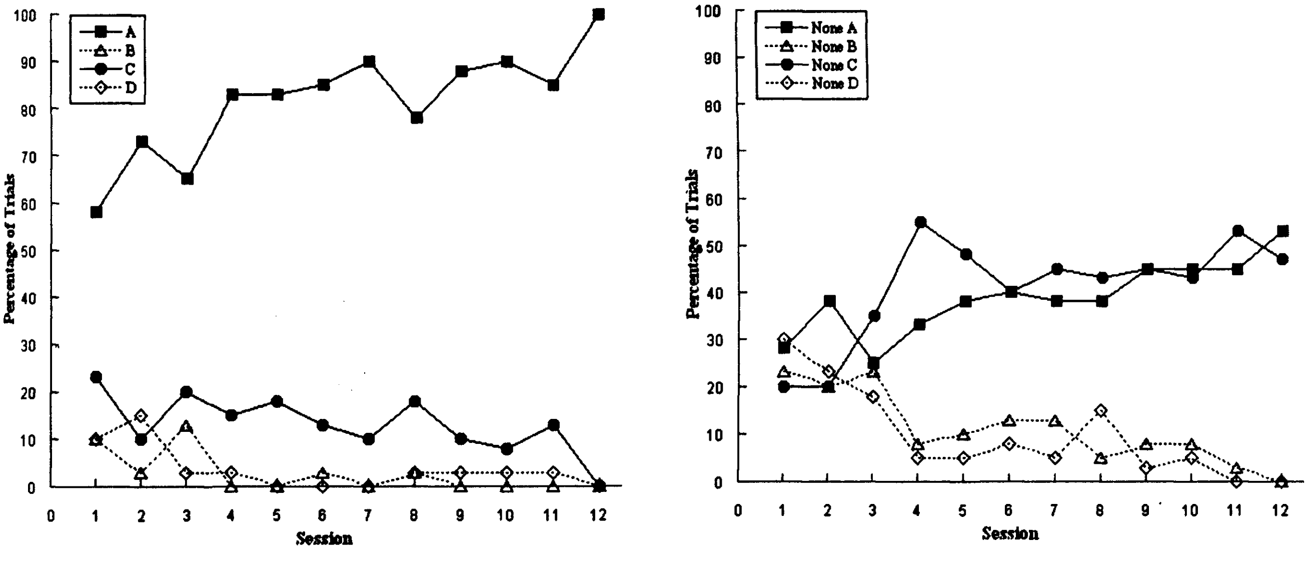

Figure 2.15. Mean percentages of trials that Group Landmark (left-hand panel) and Group None (right-hand panel) entered first each corner of the rectangular array during the acquisition stage of Experiment 4.

The mean percentages of trials on which the corner of the pool where the platform was located (A), the geometrically equivalent corner (C) and Corners B and D respectively, were entered first for the 12 sessions combined were: 81, 13, 3, 3 for Group Landmark; and 39, 41, 10, and 10 for Group None (see figure 2.15). Paired comparisons revealed that Group Landmark entered first the corner containing the platform and the landmark significantly more often than any other corner Ts (10)=0. Similar comparisons revealed that Group None entered first the corner containing the platform significantly more often than corners B and D, Ts (10)=0, but not the geometrically equivalent corner T(10) =12. Furthermore each group searched in the geometrically equivalent corner more often than either Corners B or D Ts(10)=0.

Taken together these findings confirm that Group Landmark discriminated between the corner occupied by the platform and other corners of the pool. They must have therefore used the landmark to do so. The results also reveal that Group Landmark must have referred to the shape provided by the landmark array to search for the platform. Had they not done so, errors of swimming to the geometrically equivalent corner (C) should have been roughly equal to errors of swimming to the corners B and D. In fact, Group Landmark searched corner C more frequently than either corners B or D, implying that their behaviour was, at least in part, controlled by the shape of the array. Group None failed to discriminate between the correct corner and its geometric equivalent, but they did discriminate these corners from the other two- they must have therefore found the platform by referring to the shape of the landmark array.

It is obvious from the above percentages that Group Landmark entered first the correct corner more often than Group None, which suggests that the landmark acquired considerable control over searching for the platform. In confirmation of this observation, Group Landmark entered first the correct corner significantly more often than Group None $\underline{U}(10, 10) = 3$.

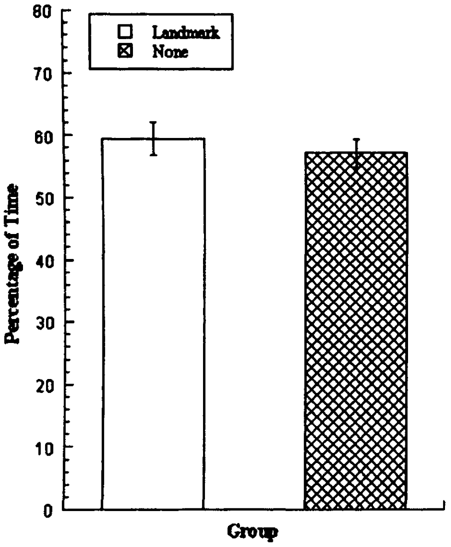

Figure 2.16. Mean percentages of time the groups spent searching in the correct regions of the rectangular-shaped array during the test without the platform and landmark for Experiment 4 (error bars represent ± 1 standard error of the mean).

The results from the test trial are shown in figure 2.16. Both groups spent more than half of their time searching in the correct quadrants of the pool. This preference was marginally greater for Group Landmark than Group None. One-sample t-tests confirmed each group spent significantly more than half of the test trial searching in the correct quadrants of the pool, $\underline{t}s(9) > 2.68$, $\underline{p}s \leq 0.01$, and a one way ANOVA confirmed that the difference between the groups was not significant, $\underline{F}(1, 18) = 0.41$, $Mse = 61.78$, $\underline{p} = 0.53$, $\eta_p^2 = 0.02$. These results confirm that both groups must have based their search for the platform on the shape of the landmark array during the first stage.

One concern with the results of the test trial is that the preference exhibited by rats for swimming in the correct quadrants of the pool was relatively poor, implying the test was insensitive to the effects of cue competition. Had cue competition been successful, however, Group Landmark should have spent significantly less than 50% of its time in the correct quadrants. The test revealed evidence to the contrary and showed that Group Landmark spent more time in the correct quadrants than Group None. The test was thus sufficiently sensitive to reveal this small difference.

The results of the test trial for Group Landmark show that learning based on the overall shape of the array was not restricted, to any degree, by the presence of the landmark near the platform during training. Numerically, this group spent marginally more time than Group None searching in the correct corners of the rectangular array. This apparent absence of competition took place despite the fact that the landmark was more reliable as a cue for finding the platform than the overall shape of the landmark array. In addition cue competition failed despite evidence showing that the landmark acquired considerable control over searching for the platform during the training stage. The present results resemble those of the first three experiments and extend them by showing that the failure of a landmark to restrict learning based on geometry is not limited to the shape provided by an enclosed environment

The main reason for conducting Experiment 4 was to assess further the idea raised earlier that previous failures to find cue competition resulted from the landmark being a relatively weak cue for finding the platform relative to the shape of a pool with enclosed walls. The current experiment used a configuration of four cylinders to create a virtual rectangle and it was intended to reduce the salience of the shape.

Under these conditions theories of associative learning (Rescorla & Wagner, 1972) predict, with some certainty, that the landmark should have restricted spatial learning based upon the shape of the pool. The results of this experiment, however, suggest otherwise.

The question remains then, did using a configuration of landmarks reduce the saliency of the shape? One way to answer this question is to compare the mean group escape latencies, over all the sessions combined, of the control group from this experiment with that of the equivalent group of Experiment 1. These means were 13.59 s and 42.8 s for the control groups of Experiments 1 and 4 respectively. These figures show that escape latencies were longer for the control group in Experiment 4 than for control group of Experiment 1. Importantly, each group had to find the platform by referring to geometric cues. In Experiment 1 these cues were supplied by the shape of an enclosed rectangular arena, whilst in Experiment 4 the configuration of landmarks provided them. The difference between the results of the experiments then, demonstrates the success of the manipulation that was intended to reduce the salience of the shape of the pool. If, for example, the salience of the landmark array was greater than the rectangular pool then escape latencies should have been considerably shorter for the group trained with the landmark configuration than the one trained with enclosed-wall arena. In fact the reverse outcome was found, which suggests that the landmark configuration was considerably less salient than the rectangular pool. Thus, the present results not only confirm the reliability and generality of the effect reported in the first experiment, they also make it unlikely that the failure of the landmark to overshadow spatial learning based on the shape of the pool, or the landmark configuration, was due to the relatively low salience of the landmark. Of course, the foregoing conclusions need to be viewed with a measure of caution. First, because it relies on a comparison across experiments and second because it relies on the assumption that escape latencies are influenced by stimulus salience. It is also worth bearing in mind that the pool used for Experiment 4 was larger in area than the ones used for earlier experiments, which may have resulted in longer escape latencies.

2.05. General Discussion

The results of the first three experiments make it unlikely that the failures to observe cue competition found here were a consequence of the low salience of the landmark relative to the shape of the triangular and rectangular pools. The outcome of the final experiment adds considerable weight to this idea. In that study four landmarks were used to create a virtual rectangle which was intended to reduce the salience of the shape, relative to the landmark, but once again cue competition failed.

Despite the foregoing results, it is possible that the landmark was, for some other reason, a poor cue for blocking and overshadowing. One possibility is that blocking may have been weakened through a generalisation decrement caused by changing the environment from a rectangular to a triangular-shaped pool and vice versa. There seems little evidence to support this idea, however. At the outset and throughout the second stages of Experiments 2 and 3 rats quickly swam toward the landmark even though the shape of the environment had changed. Moreover, an experiment by Hayward et al (2004) indicates that under the appropriate circumstances the landmark used in all four of the previous experiments can be an effective cue for blocking. They pre-trained two groups of rats to escape from a circular pool by swimming to a submerged platform that was a fixed distance and direction from the landmark. For each trial the platform with the landmark was moved to a new position in the pool with respect to the experimental room. Although rats could use the landmark as a cue to determine the distance of the platform from the landmark, they had to refer to the room cues to establish the heading between these two objects. Training rats in the manner described should thus have encouraged them to find the platform with reference to the landmark as well as room cues.

For the second stage the groups were given a final session of training that comprised four training trials and a test trial. The landmark was placed in the centre of the pool for the first four trials of the session and for the blocking group, the platform was located at the same distance and direction from the landmark as in Stage 1. Rats could thus once again identify the position of the platform by referring to the landmark as well as the room cues. However, the effects of the prior training with the landmark might be expected to block (Kamin, 1969) learning to locate the platform with reference to the room cues (see Roberts & Pearce, 1999).

During the final session of training and for the control group, the platform was located at the same distance from the landmark, but in the opposite direction to that used for the previous stage. Consequently it was not possible to escape from the pool by referring to the landmark. Instead the control group was expected to find the platform by referring to the room cues. To assess these possibilities, a test trial, conducted without the landmark and the platform but in the presence of the room cues, showed that the blocking group spent significantly less time than the control group searching in the region of the pool previously occupied by the platform.

The outcome of the test for the blocking group implies that learning to locate the platform with reference to the landmark during Stage 1 restricted learning to locate it with reference to the room cues during Stage 2. Thus there appears to be some circumstances, at least, where the landmark used in the previous experiments can influence spatial learning. As such it would be unreasonable to attribute the absence of blocking and overshadowing in those experiments to some inherent property of spherical landmark that rendered it unsuitable for revealing the effects of cue competition.

The current experiments extend the conclusions that can be drawn from previous failures of a landmark to overshadow spatial learning based on the shape of the environment in several important ways. In the experiments reported by Pearce et al (2001), rats were required to find a submerged platform in a triangular-shaped pool containing three different corners, which meant that the corner in which the platform was located and the landmark were equally reliable as cues for locating the platform. By using a rectangular pool, the first experiment showed that a landmark will fail to overshadow learning about the shape of the environment, even when it is a more reliable cue for finding the platform than the corners of the rectangular pool.

The experiments also extend the conclusions that can be drawn from previous studies by allowing comparisons to be made between the salience of the landmark and the shape of the pool. The results from the initial training stages of Experiments 2 and 3 show that the salience of the landmark was not less than the shape of either the rectangular or the triangular pool. It thus becomes difficult to explain the failures of overshadowing and blocking in the first three experiments in terms of the landmark being a much weaker cue for spatial learning than the shape of the pool.

The results of the final experiment are worthy of further consideration. In that study the salience of the rectangular shape is likely to have been reduced by creating it from four identical cylinders. The landmark was thus not only a more reliable cue for finding the platform but it was also more salient than the shape of the pool. According to theories like the Rescorla-Wagner model (1972) the greater reliability and salience of the landmark should have ensured it became an effective cue for finding the platform and increased the likelihood of its restricting learning based on the shape of the array. The results of the final experiment, however, failed to confirm this prediction and revealed no evidence of cue competition. These results are thus more difficult for associative learning theories (Rescorla & Wagner, 1972) to explain than many of the previous failures to find cue competition.

Attempting to demonstrate that a landmark does not restrict learning based on the shape of the environment suffers from the inevitable problems associated with trying to confirm the null hypothesis. However, by showing that the effects reported by Pearce et al (2001) can be obtained with a landmark that is some distance from the platform, and in a rectangular rather than a triangular-shaped pool, the present results extend the conditions under which a failure of a landmark to restrict spatial learning based on the shape of the environment has been found. Extending the generality of the absence of an effect does not confirm the null hypothesis, but it does suggest that it is worth considering the possibility that learning about the shape of the environment is not affected by the presence of landmarks within it. It is noteworthy that in each experiment there was not even a numerical hint that the landmark detracted from learning about the shape of the pool. Indeed, in several instances, numerical differences pointed to the opposite conclusion.

The designs of the experiments were conducted with theories of associative learning in mind (e.g. Mackintosh, 1975; Pearce & Hall, 1980l; Rescorla & Wagner, 1972). These theories predict that cue competition effects are more likely to be seen when the stimuli differ in salience, or when they differ in their relative validity as signals for reward, or when pre-training has been conducted with one stimulus but not the other. Although none of these predictions were confirmed, it may still be premature to conclude that theories of associative learning do not apply to learning based on the shape of the environment. One avenue that might be worth pursuing, if the present results are to be reconciled with associative learning theory, can be based on the fact that cue competition effects are normally studied with stimuli that are presented together simultaneously. The nature of the task employed in the present experiments might, however, have encouraged subjects to attend to the relevant stimuli one at a time. In Experiment 1, for instance, rats may have first headed for the landmark and upon reaching it then headed for the corner of the pool. If the platform was discovered while they were heading for and paying attention to the corner, then it is conceivable that the landmark would exert little influence on learning about the significance of the shape of the pool. There are several reasons for treating this explanation with caution. First, it implies that the landmark will gain little control over searching for the platform, because it will be overshadowed by the shape of the pool. However, this claim is challenged by the findings from each of the first three experiments. Not only did these experiments provide clear evidence of the landmark acquiring control over searching for the platform, they also revealed that the landmark was a more effective cue than the shape of the pool for finding the platform. Second, in an experiment based on the design of Experiment 1, I have found that black cards (20 cm by 20 cm) pasted on the white walls in one corner of a rectangular pool exert no influence on the control acquired by the shape of the pool over searching for a platform located in the same corner. It seems likely that the cards would be perceived at the same time as the relevant information about the shape of the correct corner, so that theories of cue competition would be expected to apply under these conditions.

Finally the results of an experiment conducted by Kehoe (1982) show that it is possible to obtain cue competition effects even when stimuli are presented sequentially rather than simultaneously. In that experiment rabbits received trials in which the sequence of A followed by B was followed by an unconditioned stimulus. The control acquired by B over responding was substantially diminished if A was paired with the unconditioned stimulus before the start of serial conditioning.

It also noteworthy that Hayward et al (2004) showed that the landmark identical to the one used for these experiments did block learning based on the cues surrounding the pool. This finding confirms that at least in some conditions the method of testing was sufficiently sensitive for revealing cue competition effects. It also implies that an intramaze landmark will compete for control over searching with cues surrounding a pool, but not with the shape of a pool. Whether cue competition might be found between the shape of the pool and the cues surrounding it remains to be seen, and the following chapter is aimed at assessing this possibility.

In contrast to the problems posed by the present results for associative learning theory, the failures of the landmark to restrict learning based on geometric properties provided by the shape of the pool, is entirely consistent with the theory of the Cheng's Geometric Module (Cheng, 1986; Gallistel, 1990), which asserts that landmarks and geometry are processed independently. The special status that is afforded to the shape of the environment for spatial learning by Cheng and Gallistel provides a simple framework for understanding the present results as well as those from related studies (Cheng, 1986; Kelly et al 1998; Pearce et al 2001; Tommasi & Vallortigara, 2000; Vallortigara et al 1990). The purpose of the following experiments is to examine in more detail the conditions under which failures to observe cue competition occur.

Chapter 3.

Failures of Room Cues to Restrict Spatial Learning based on the Distinctive Shape of a Pool.

So far my experiments have shown that learning based on the distinctive shape of a pool is neither overshadowed by nor blocked by an intramaze landmark. Such failures could not be explained readily in terms of the landmark being less salient than the shape of the pool and thus do not sit comfortably with theories of associative learning (Rescorla & Wagner, 1972; Mackintosh, 1975). They are, however, in agreement with the Geometric Module theory of spatial learning (Cheng, 1986; Gallistel, 1990) which asserts that information about the shape of an environment is stored in a dedicated module, impenetrable to featural cues such as landmarks.

If there is any generality to the proposals made by Cheng (1986) and Gallistel (1990) then other featural cues, such as those provided by an experimental room, might also fail to restrict learning based on the shape of an environment. Assuming it is appropriate to extend the theory of the Geometric Module in this way; then such expectations not only contravene the general mechanism of cue competition described by the Rescorla-Wagner model (1972) but they also contradict the available empirical data.

There is much evidence to suggest, for example, that spatial learning based on intramaze cues can be overshadowed by (Chamizo et al, 1985; March et al, 1992; Roberts & Pearce 1998) and blocked by extramaze cues (Chamizo et al, 1985). In one such study Roberts and Pearce (1998) trained two groups of rats to escape from a circular pool filled with opaque water by finding a submerged platform. The platform was always located at a constant distance and direction from a spherical landmark and the room cues were visible by rats swimming around pool. For Group Fixed, the platform and landmark remained in the same place with respect to the room cues throughout training. They could thus find the platform by referring to the room cues as well as the landmark. For Group Varied, the platform with the landmark was moved to a new position in the pool with respect to the room cues for each trial- encouraging rats to find the platform with reference to the landmark. Subsequently rats were released in the pool without the platform or landmark but in full view of the room cues, thereby extinguishing any control the room cues had acquired over searching.

At the end of the experiment rats received a test trial during which the platform and the landmark occupied a novel location with respect to the room cues. The results of the test showed that Group Fixed took longer to escape onto the platform than Group Varied. It is thus apparent that the room cues restricted to a greater extent the control acquired by the landmark in Group Fixed than Group Varied. Put simply, learning based on the landmark seems to have been overshadowed by the room cues.

Unfortunately, not one study to date has tested whether the cues located outside an environment might restrict learning based on its shape. In the experiment by Margules and Gallistel (1988), mentioned earlier, an experimental group of rats was trained to find a goal in one corner of a rectangular arena. Despite the absence of features within the arena, rats reliably disambiguated the corner with the goal from the geometrically equivalent corner. They must have therefore referred to the cues provided by the experimental room which surrounded, and could be seen from the apparatus. The behaviour of rats was thus controlled to some extent by the room cues. Whether such control was sufficient to restrict learning based on the rectangular arena is impossible to determine, however, because the experiment included neither the appropriate tests nor controls. Although far from conclusive, the study by Margules and Gallistel (1988) hints at the possibility that under the right conditions competition might be observed between the shape of an environment and the cues surrounding it. The primary purpose of the forthcoming experiments was to test this idea.

The organisation of this chapter is much the same as the previous one. The first three experiments were designed to test whether the cues provided by an experimental room might overshadow spatial learning based on the distinctive shape of a pool. In each experiment, an experimental group of rats was trained to swim to a submerged platform which could be found by referring to the shape of a pool as well the room cues which surrounded the apparatus. Given that such conditions are theoretically sufficient to demonstrate overshadowing (Rescorla & Wagner, 1972); then learning based on the room cues might restrict and be restricted by the shape of pool. If, however, there is any merit to the proposals of Cheng (1986) and Gallistel (1990), or any generality to the findings of the previous four experiments, then there are no grounds for supposing that competition should occur.

If the room cues should fail to restrict learning based on the shape of the pool then there is at least one way in which associative learning theory (Rescorla & Wagner, 1972) might explain the absence of cue competition. The room cues would be relatively ineffective for overshadowing if they were much less salient than the shape of the pool (Mackintosh, 1975; Pearce & Hall, 1980; Rescorla and Wagner, 1972) and Experiment 6 is particularly relevant to this issue of stimulus salience.

3.01. Experiment 5a

Experiments 5a and 5b were conceptually identical and were designed to test whether learning based on the shape of the pool might be overshadowed by the presence of room cues. In the first experiment, training took place in a rectangular pool, whilst in the second a triangular-shaped pool was used. The purpose for conducting two experiments was that if they should reveal the same results then the conclusions that can be drawn from them will be more forceful than if only a single experiment was conducted. Moreover, because environments of different shapes were used, the outcome of the second experiment might be used to extend the generality of the results provided by the first experiment and vice versa.

For the current experiment, two groups of rats were trained to escape from a rectangular pool which was identical to the one used for Experiment 1. In contrast to the previous studies a landmark was never placed in the pool. Moreover, the cues of the experimental room could be observed by rats swimming in the pool because the curtain which had surrounded the apparatus in the previous studies remained open. For Group Stable, the orientation of the pool remained constant and the platform could always be found in the same corner of the rectangular pool. As a result the room cues, rather than the shape of the pool, could be used to predict accurately the location of the platform. The control group, Group Rotate, was treated identically to Group Stable except for these rats the orientation of the rectangle was changed for each trial, making the room cues ineffective for finding the platform. Instead the geometric cues provided by the rectangle had to be used to escape from the pool.

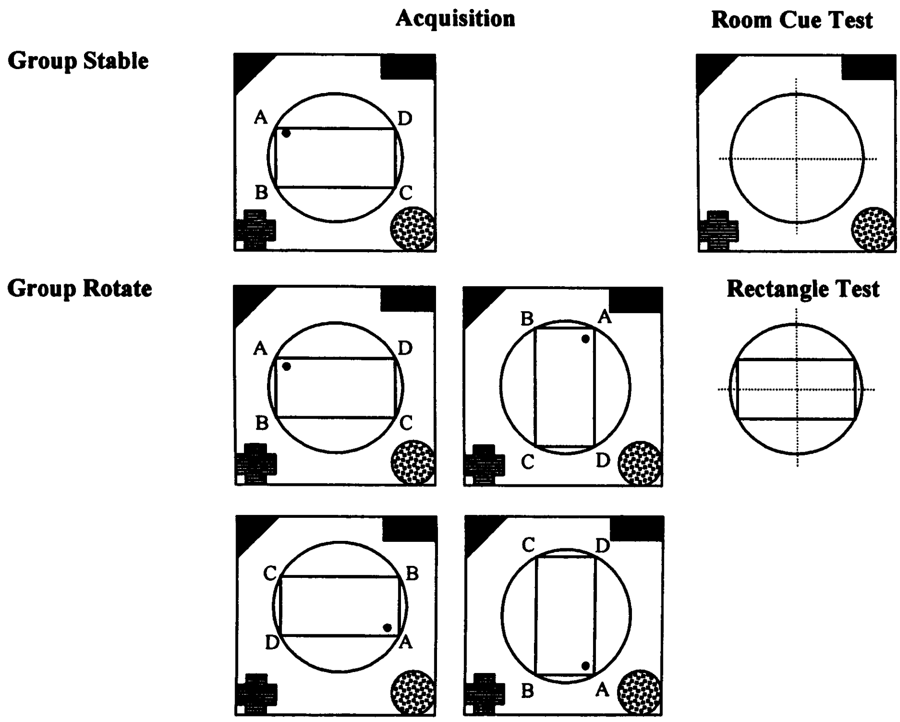

Figure 3.01. The apparatus and design adopted for Experiment 5a. Filled circles show the position of the platform. The geometric shapes in the corners of the square surrounding the pool represent the cues provided by the experimental room.

Given the novelty of Experiment 5a it is perhaps difficult to know whether training Group Stable to find the platform with reference to the room cues and the shape of the pool would result in these cues competing for the control they acquired over searching. From the perspective of associative learning theories (Rescorla & Wagner, 1972) competition is expected because the room cues were more reliable for finding the platform than the rectangle's corners. The available empirical data leads to much the same prediction. Experiments have shown, for instance, that the presence of room cues can not only restrict learning based on intramaze cues (Chamizo et al, 1985; March et al, 1992; Roberts & Pearce 1998) but they can also be used by rats to disambiguate geometrically equivalent corners of a rectangular arena devoid of features (Margules & Gallistel, 1988). It remains a possibility therefore that room cues might, under the circumstances described, restrict spatial learning based on the shape of pool.

Alternatively, if there is any generality to the effects described in the previous chapter or any merit to the ideas expressed in the theory of the Geometric Module (Cheng, 1986; Gallistel, 1990); then there is no reason to suspect that the presence of the room cues should influence, to any degree, learning based on the rectangular pool in Group Stable.

To test the above predictions rats received a test trial during which they were placed in the rectangular pool without the platform. For the test the curtain was drawn around the pool to occlude the room cues which rendered them ineffective for finding the platform. Spatial learning based on the shape of the pool was assessed by recording the percentage of time rats spent searching in the quadrant previously occupied by the platform and the geometrically equivalent quadrant. Together these two quadrants were considered to be the geometrically correct ones.

Evidence that learning based on the shape of the pool had progressed normally in Group Stable would be revealed by these rats exhibiting a similar preference for searching in the geometrically correct quadrants of the pool than the group who were trained with the rotating rectangle. Any evidence of overshadowing by the room cues on the rectangular pool would be revealed by Group Stable showing only a weak preference for swimming in the geometrically correct quadrants compared to the control group.

Subsequent to a further session of training with the rectangular pool, rats were given an additional test that was conducted in the circular pool with the curtains open, but in the absence of the rectangle and platform. The primary purpose of this test was to examine the extent to which Group Stable relied on the cues surrounding the pool to find the platform. As with the previous test a record was taken of the time rats spent swimming in the quadrant of the pool previously occupied by the platform.

Method

Subjects and Apparatus The 20 rats were of the same stock, with similar experience, of approximately the same age, and housed in the same conditions as those from the previous experiments. At the start of the experiment the rats were assigned randomly to two groups of equal number. The rectangular arena was identical to the one used for Experiment 1. There was a door in the centre of one wall of the experimental room and for the purposes of the experiment the centre of the door was defined as South.

Attached to the walls of the experimental room were 8 large posters (see figure 3.02). On the North wall there was black triangle (A), inverted so that its apex pointed down toward a book shelf (B), measuring 1.8 m high, 1 m wide and 0.3 m depth, which stood beneath it in the North-East corner. At the centre of the East wall and with its length hung vertically was a rectangle with black and white vertical stripes (D). On the left-hand side of the latter object was a grey circle centred on black rectangular background (C) and on its right-hand side was a black irregular octagon (E). There were no posters on South wall, but the South-East corner was occupied by equipment needed to maintain a clean laboratory. At the centre of the West wall was a black circle with semi-circular petal-like projections placed around and touching its circumference every 45° (G). On the left-hand side of this object and hung with its length horizontally was a white rectangle which had a black cross bisecting its corners (F). Finally, in the North-East corner the apexes of two equilateral triangles met. Each was identical and had black and white horizontal stripes (H). The curtain remained open throughout experiment (J). Together all these objects and everything else in the experimental room shall be referred to as the room cues.

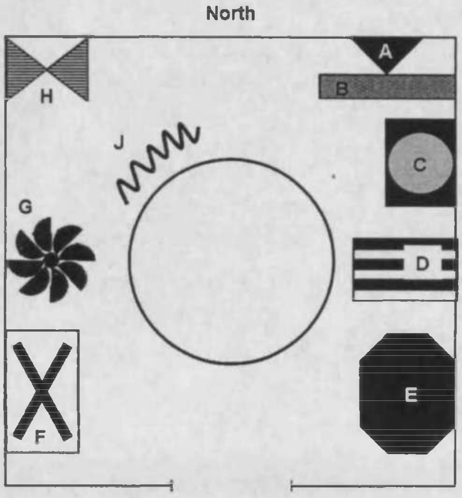

Figure 3.02. Plan view of the experimental room showing the arrangement the wall posters, curtain and pool (not drawn to scale, see text for details).

Procedure During acquisition trials each group was required to escape onto a submerged platform that was located 30 cm away from the corner of the rectangular pool. The method used for positioning the platform was identical to that used for Experiment 1. Half the subjects in each group were trained with the platform in a corner with the short wall to the left of the long wall, whilst for the remaining subjects the other corners were used. For Group Rotate, within a session, the platform was located twice in each geometrically equivalent corner of the rectangle and was moved between these corners in a random sequence. In contrast the platform remained in the same corner for Group Stable and the rectangle, which remained stationary, was always oriented along the East-West axis of the pool. For Group Rotate the rectangle was oriented twice within each session along the North-South axis and twice along the East-West axis and was moved between these positions in random sequence. This method meant that the platform, for Group Rotate, occupied four different locations with respect to the room, in each session.

The first three trials of session 12 were conducted in the same manner as all other training trials. On the fourth test trial the platform was removed from the pool and the rectangle was oriented on the North-South axis. For the duration of the test trial the curtain was pulled completely around the pool to occlude the cues of the experimental room. For the purposes of the test the rectangular pool was divided into four quadrants of equal size and the time spent in the correct quadrants of the pool was recorded. The correct quadrants were the quadrant of the pool previously occupied by the platform and the corner diametrically opposite to it.

Subsequent to the second test the groups were given a further session of training. During session 14, the first three trials were conducted in the same manner as all other training trials. On the fourth test-trial the platform and the boards that the rectangle was constructed from were removed from the pool. For the purpose of the test the circular pool was divided along the North-South and East-West axis into four quadrants of equal size and the time that rats spent searching in the correct quadrant of the pool was measured. For Group Stable the correct quadrant was considered to be that previously occupied by the platform. The same quadrant was used to assess the performance of Group Rotate. All other procedural details for the test that have been omitted were identical to those of the first test trial.

Results and Discussion

The type 1-error rate of p<0.05 was the same in this chapter as for the previous one. The group mean escape latencies for acquisition trials from the 14 sessions of the experiment can be seen in figure 3.03.

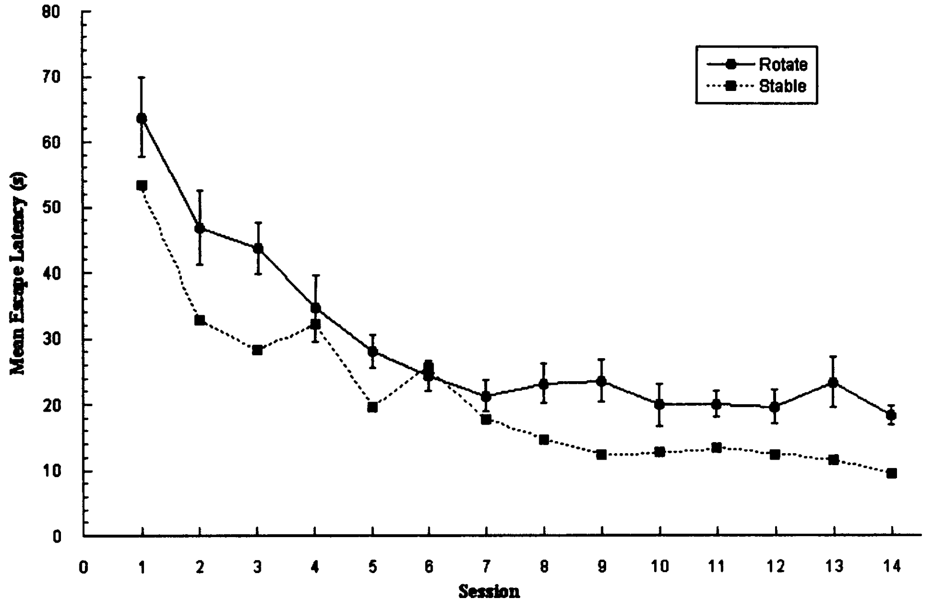

Figure 3.03. Mean escape latencies for the groups during the acquisition stage of Experiment 5a (error bars represent ±1 standard error of the mean).

Training was more successful with Group Stable than with Group Rotate, which suggests that the former group made use of the room cues to find the platform. A mixed two-way ANOVA of escape latencies over the 14 sessions of training for the groups showed a significant effect of group, F(1, 18)= 31.10, Mse= 152.72, p= 0.00, η_p^2= 0.633, and of session, F(13, 234)= 29.80, Mse= 105.89, p= 0.00, η_p^2= 0.54, but the interaction of Group x Session was not significant, F(2, 234)= 0.97, Mse= 105.89, p= 0.49, η_p^2= 0.04.

In addition to noting escape latencies, a record was taken on every trial of which corner a rat entered first after being released into the rectangular pool. This was done to assess the degree to which rats relied on the room cues for finding the platform. The corner containing the platform was assigned the letter A, the geometrically equivalent corner, C, and the remaining incorrect corners B and D (see figure 3.01). For every session the mean percentage of trials on which individual rats from each of the two groups first entered each corner was calculated.

Figure 3.04 (left-hand panel) shows the mean percentage of trials on which Group Stable entered first each corner after being released into the rectangular pool. Upon being released, rats swam directly to the corner containing the platform on the majority of trials in every session except for the first three. This pattern of results confirms rats learned to use the room cues to find the platform. On the remaining trials rats tended to swim towards the corner diametrically opposite to the one containing the platform which suggests they also found the platform by referring to the shape of the pool, despite the presence of the room cues. There were very few occasions particularly towards the end of training when rats swam to the remaining corners first.

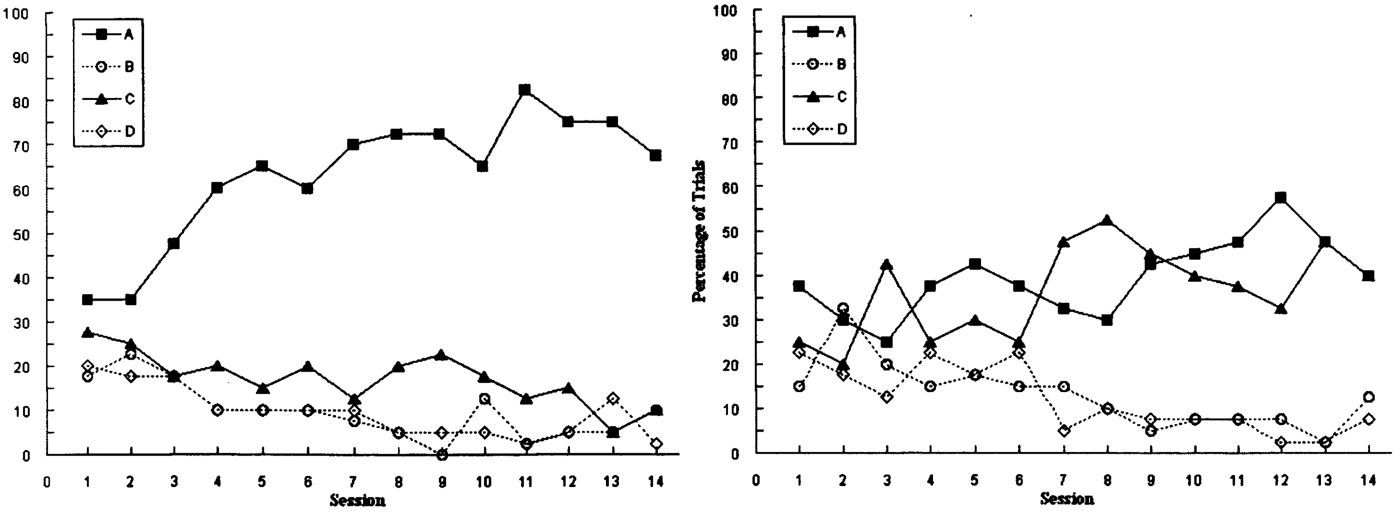

Figure 3.04. Mean percentages of trials that Group Stable (left-hand panel) and Group Rotate (right-hand panel) entered first each corner of the rectangular pool during the acquisition stage of Experiment 5a.

In corroboration of the preceding observations within group comparisons revealed that for the 14 sessions combined Group Stable entered the corner containing the platform significantly more often than any other corner, Ts (10)=0. In addition entries to the geometrically equivalent corner were significantly greater than the remaining corners of the pool, Ts (10)≤3. There are two major implications of these results. First, they show that Group Stable successfully discriminated the corner with the platform from the geometrically equivalent corner, which implies the room cues acquired some control over their behaviour. In addition, the shape of the pool must have also controlled searching for the platform because this group made more errors of swimming to the geometrically equivalent corner than to remaining corners of the pool.

Figure 3.04 (right-hand panel) illustrates the equivalent results for Group Rotate and shows that on the majority of trials rats searched the corner with the platform and the one geometrically equivalent to it. The remaining incorrect corners were entered first rather infrequently, particularly towards the end of training. These results suggest that Group Rotate used the shape of the pool to find the platform. In support of these observations within-group comparisons revealed that for the 14 sessions combined, rats entered first the corner with the platform and the geometrically equivalent corner equally often, $\underline{T}$s (10)=8. Rats swam to each of the correct corners more frequently than the two incorrect corners of the pool, $\underline{T}$s (10)=0. These results confirm that Group Rotate found the platform with reference to the shape of the pool.

The mean percentages of trials on which individual subjects swam directly to corners A, B, C and D for the 14 sessions combined were: 63, 10, 18, and 9, for Group Stable; and 39, 13, 36, and 12, for Group Rotate. A comparison of these means showed that the percentages of trials the groups entered first corners A and C combined did not differ, $\underline{U}$(10, 10)=89. Group Stable entered the corner with the platform (A) significantly more often than Group Rotate, $\underline{U}$(10, 10)=6. The latter finding reinforces the idea that Group Stable must have referred to the room cues to disambiguate corner A from C.

The mean percentages of time spent in the correct quadrants of the pool during the 60-s test trial with the rectangular pool and with the curtains closed are shown in figure 3.05 (left-hand side). One sample t-tests revealed that Group Rotate spent significantly more than 50% of its time searching the correct quadrants of the pool, $\underline{t}$(9)= 5.60, $\underline{p}$= 0.00, as did Group Stable, $\underline{t}$(9)= 4.86, $\underline{p}$= 0.00. A one-way ANOVA of time spent in the correct quadrants showed that the groups did not differ $\underline{F}$(1, 18)= 0.12, Mse=97.72, $\underline{p}$= 0.74, η_p^2=0.00. Together these results provide evidence to suggest that the presence of the room cues failed to influence spatial learning based on the rectangular pool in Group Stable. In short, it seems that the room cues failed to restrict learning based on the rectangular pool.

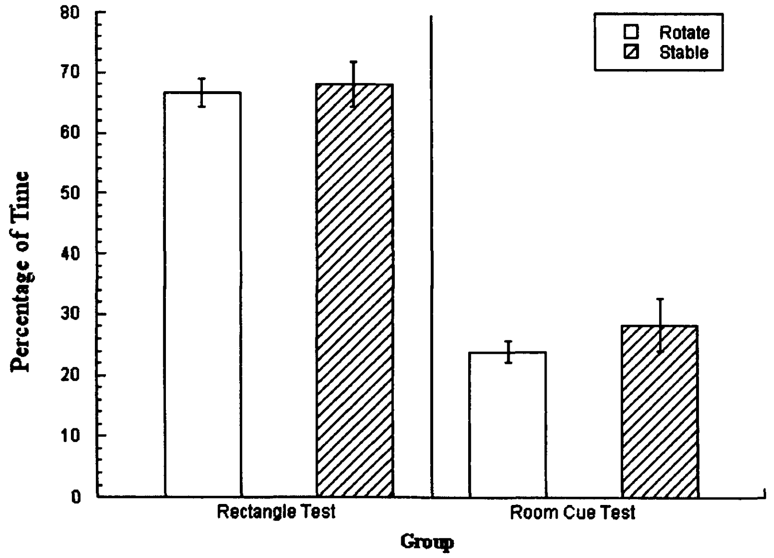

Figure 3.05. Mean percentages of time the groups spent searching in the correct quadrants of the rectangular (left-hand side) and circular pools (right-hand side) during the test trials conducted without the platform.

Figure 3.05 (right-hand side) illustrates the results of the second test trial that took place in the circular pool with the curtains open. One sample t-tests revealed that the Group Rotate ($t(9) = -0.531$, $p = 0.61$) as well as Group Stable ($t(9) = 0.80$, $p = 0.44$) failed to spend more than 25% of their time searching the correct quadrant of the pool: that previously occupied by the platform. A one-way ANOVA of time spent in the correct quadrant showed that the groups did not differ $F\ (1, 18) = 0.90$, Mse= 108.81, $p = 0.36$, $\eta_p^2 = 0.05$. The outcome of the test for Group Rotate is perhaps unsurprising because the room cues could not be used by rats for finding the platform during acquisition. The result of the test for Group Stable, however, is surprising because there is sufficient evidence to suggest that these rats used the room cues in addition to the shape of the pool to find the platform during acquisition.

Despite the fact that Group Stable could find the platform by referring to the room cues, the experiment provides clear evidence to suggest that the rectangular pool was also used by rats to identify the position of the platform. This evidence is apparent in the results of the training stage which revealed that rats swam first not only to the corner containing the platform, but also to the geometrically equivalent corner. Further evidence to illustrate that Group Stable referred to geometric cues is provided by the first test trial which took placed in the rectangular pool and with the curtains closed. In that test Group Stable exhibited a similarly strong preference for the geometrically correct quadrants as Group Rotate which implies the room cues had little impact on conditioning with the rectangular pool.

In the context of associative learning theory (Rescorla & Wagner, 1972) the latter conclusion is somewhat surprising because the room cues were more reliable than the shape of the pool for finding the platform. Under such conditions associative learning theory (Rescorla & Wagner, 1972) predicts that the former should have overshadowed the latter. Clearly this did not occur. As a result theories like the Rescorla-Wagner (1972) do not seem to provide an adequate explanation for the current results.

Evidence that the room cues were used by Group Stable to find the platform is rather mixed. On the one hand the results from the acquisition stage of the experiment show without much doubt that Group Stable must have used the room cues to search for the platform because rats swam to the correct corner significantly more often than any other corner of the pool. Unfortunately, the percentage of time these rats spent searching in the correct quadrant of the circular pool during the test with curtains open, in full view of the room cues, did not differ from that exhibited by Group

Rotate. This result implies that any control acquired by the room cues over searching for the platform in Group Stable was rather weak. The critical question to ask is how might such a paradox be explained? To save repetition suitable answers to this question shall be provided after the next experiment has been presented because a similar situation arose in that study.

What is clear from the present experiment is that the room cues had no influence on learning to locate the platform with reference to the shape of the pool. Not only are such conclusions consistent with the results of the experiments included in the previous chapter but they are also in harmony with theories of spatial learning such as the Geometric Module (Cheng, 1986; Gallistel, 1990).

3.02. Experiment 5b

The design and rationale to this experiment was the same as for the previous one except that the two groups were trained to find a submerged platform located in one corner of triangular-shaped pool with a curved base, rather than a rectangular pool. As before the room cues could be viewed by rats as they swam around the pool. For Group Stable the orientation of the triangle remained constant with respect to the room cues, whilst for Group Rotate four orientations were used and the triangle was moved between them for each trial.

After successful completion of the training stage the groups were given a test trial which was conducted in the triangular-shaped pool with the curtains drawn around it but without the platform. Should overshadowing of the triangular-shaped pool by the room cues be successful, then Group Stable would not be expected to exhibit any preference for searching in the correct quadrant of the triangle. If however, there is any generality to the results of the previous experiment, then there is no reason to anticipate cue competition and the groups should show a similarly strong preference for searching the correct quadrant during the test.

Subsequent to a further session of training with the triangular-shaped pool, the experiment concluded with a test carried out in the circular pool with the curtains open but without the platform. As with the previous experiment the purpose of this test was to examine the degree to which the room cues acquired control over searching for the platform in the group for whom the orientation of the triangle remained stable.

Method

Subjects and Apparatus The 20 rats were of the same stock, with similar experience, of approximately the same age and housed in the same conditions as those from the previous experiments. At the start of the experiment the rats were assigned randomly to the two groups. The triangular-shaped arena was identical to the one used for Experiment 2. Details of the experimental room were identical to the previous experiment.

Procedure The groups were required to escape from a triangular-shaped pool by swimming to a single submerged platform that was always located in one corner at the base of the triangle. The method used for positioning the platform was the same as that used for Experiment 2. Half the rats were trained with platform in the left-hand corner at the triangle's base, whilst for the other half it was located in the opposite corner. The curtain remained open throughout acquisition trials and from the pool rats could view the cues provided by the experimental room. For Group Rotate, the triangle was rotated from trial to trial, so that its apex pointed once toward either, North, East, South and West in each session. The triangle remained stationary for the remaining group and its apex always pointed North in relation to the experimental room. All other procedural details for the acquisition stage of the experiment were identical to other experiments that used the triangular-shaped pool (see Experiment 2).

In Session 12, the first three trials were conducted in the same manner as all other training trials. On the fourth test-trial, the platform was removed from the pool and for the duration of the test the curtain remained closed. The triangular-shaped pool was oriented for the test, so that its apex pointed toward South in relation to the experimental room. In addition it was divided into four quadrants of unequal size along the North-South and East-West axes of the pool and the time spent in each of the quadrants was measured. A rat was regarded as searching in the correct region of the pool whenever it entered the quadrant of the pool previously occupied by the platform. All other details of the test trial that have been omitted were identical to those included in previous chapters that used a triangular-shaped pool (see Experiment 2).

Subsequent to the first test the groups were given a further session of training with the triangle. During Session 14, the first three trials were conducted in the same manner as all other training trials. On the fourth test-trial the platform and the boards the triangle was constructed from were removed from the pool. For the purpose of the test, the circular pool was divided into four quadrants of equal size along the North-South and East-West axis of the pool and the time spent in each of these quadrants was recorded. Rats from Group Stable were regarded as searching in the correct region of the pool whenever they entered the quadrant previously occupied by the platform. The same quadrant was used to assess the performance of the Group Rotate. The curtains were open for the duration of the test. All other procedural details for the test that have been omitted were identical to the previous experiment.

Results and Discussion

The group mean escape latencies for the acquisition trials that took place in the triangle during the first 14 sessions of the experiment can be seen in figure 3.06. As with the previous experiment training was more successful with Group Stable than with Group Rotate, which suggests that the former group made use of the room cues as well as the geometry of the triangular-shaped pool to find the platform. In confirmation of this observation a mixed two-way ANOVA of escape latencies over the 14 sessions for the groups showed a main effect of group, $\underline{F}(1, 18)=14.81$, Mse=263.34, $\underline{p}= 0.00$, $\eta_p^2=0.45$, and of session, $\underline{F}(13, 234)=37.60$, Mse=83.19, $\underline{p}= 0.00$, $\eta_p^2=0.08$, but the interaction of Group x Session was not significant $\underline{F}(13, 324)=0.71$, Mse=83.19, $\underline{p}= 0.75$, $\eta_p^2=0.04$.

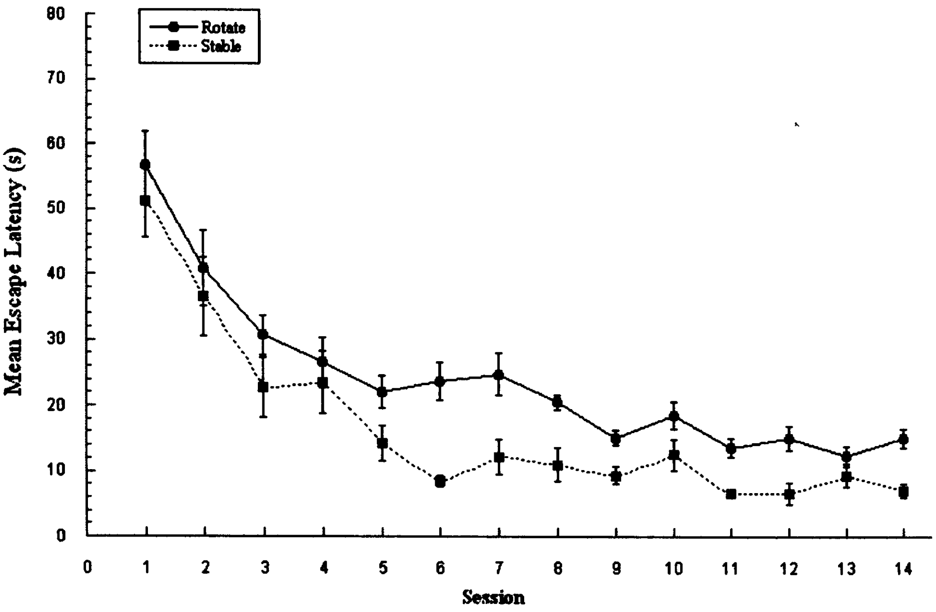

Figure 3.06. Mean escape latencies for the groups during the acquisition stage of Experiment 5b (error bars represent ±1 standard error of the mean).

Figure 3.07 shows the mean percentage of trials on which the groups swam first to the corner of the pool with the platform. The figure makes clear that training was more successful with Group Stable (left-hand panel) than with Group Rotate (right-hand panel), which once again suggests the former group referred to the room cues as well as the shape of the pool to find the platform. To evaluate this observation, a between-group comparison was made using the mean numbers of trials on which subjects swam directly to the correct corner, over 14 sessions combined. This comparison revealed that Group Stable entered first the correct corner significantly more often than Group Rotate, U(10, 10) =11.

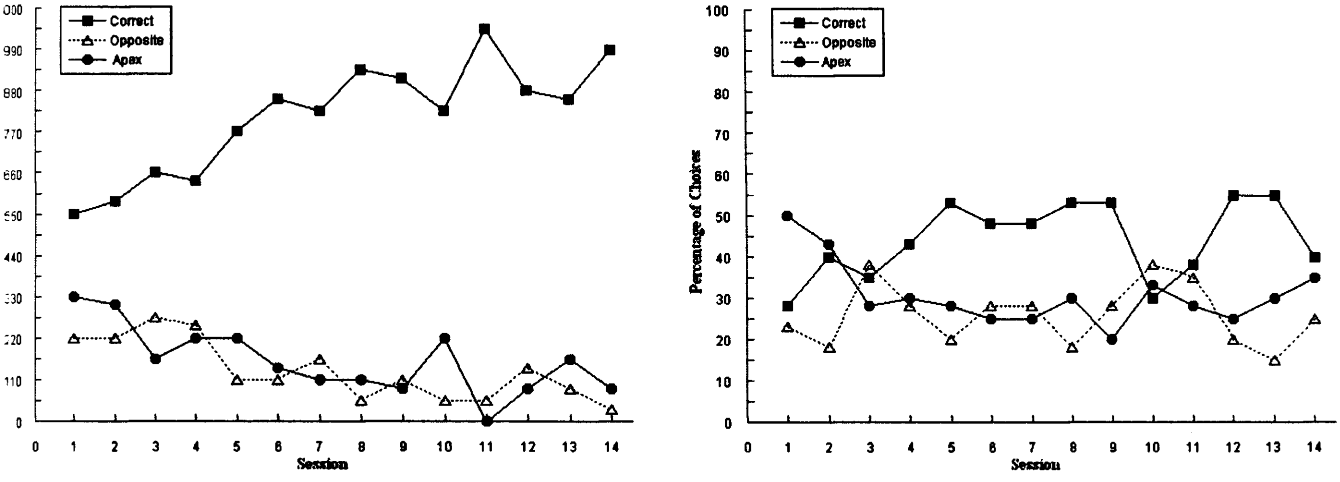

Figure 3.07. Mean percentages of trials that Group Stable (left-hand panel) and Group Rotate (right-hand panel) entered first each corner of the triangular-shaped pool during training.

The mean percentages of trials on which the corner of the pool where the platform was located, the opposite corner and the apex were entered first for the 14 sessions combined were: 73, 13 and 14, for Group Stable; and 44, 26 and 30, for Group Rotate. Paired comparisons revealed that for each group the correct corner was entered first significantly more often than either the opposite corner or the apex, Ts (10)≤8. These findings confirm that each group was able to discriminate the correct corner, where the platform was located, from the other two corners of the triangular-shaped pool.

The mean percentages of time spent in the correct and incorrect quadrants of the pool during the 60 s test conducted in the triangular-shaped pool with the curtains closed are shown in figure 3.08 (left-hand panel). Each group exhibited a strong preference for searching in the correct over the incorrect quadrant and between group differences were not apparent. A two-way ANOVA of the groups and of time spent in the correct and incorrect quadrants showed a significant main effect of quadrant, F(1, 18)= 65.33, Mse= 205.90, p= 0.00, η_p^2= 0.78. However neither the main effect of group F(1,18)=

0.01, Mse= 69.50, p= 0.91, η_p^2= 0.00) nor the interaction of Group x Quadrant, F(1, 18)=0.19, Mse= 205.90, p= 0.66, η_p^2= 0.01 were significant. These results suggest that for Group Stable learning based on the triangular-shaped pool was not restricted by the presence of the room cues.

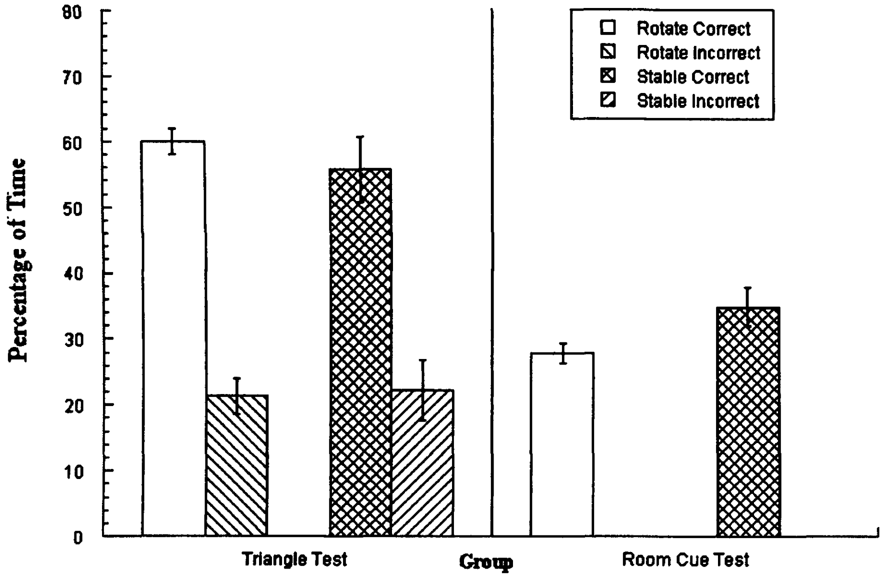

Figure 3.08. Mean percentages of time the groups spent searching in the correct and incorrect quadrants of the triangular-shaped pool (left-hand side) and correct quadrant of the circular pool (right-hand side) during the test trials conducted without the platform.

The mean percentages of time rats spent searching in the correct quadrant of the circular pool during the 60 s test trial with the curtains open are shown in figure 3.08 (right-hand side). One sample t-tests revealed that Group Stable spent more than 25% of its time searching in the correct quadrant during the test, t(9)=2.90, p= 0.01, whilst Group Rotate failed to do so t(9)=1.95, p= 0.04. A one-way ANOVA of the percentage of time spent searching in the correct quadrant of the pool showed that the difference between the groups was not significant, F(1, 18)= 3.64, Mse= 68.99, p=0.07, η_p^2=0.17.

Despite the fact that Group Stable could refer to the room cues, there is clear evidence to suggest that this group also used the geometric cues provided by the shape of the pool to find the platform. This evidence is provided by the results of the test in the triangular-shaped pool with the curtains closed, which revealed that Group Stable showed a significant preference for searching in the correct over the incorrect quadrant of the pool. Moreover, this preference of Group Stable for searching in the correct quadrant did not differ from that exhibited by Group Rotate which implies that the presence of the room cues failed to detract from learning to locate the platform with reference to the triangular-shaped pool. In short the room cues failed to overshadow learning based on the triangular-shaped pool.

It is perhaps worth mentioning that the failure of the room cues to overshadow learning based on geometry found in this experiment is less striking than the failure to find cue competition in the previous experiment. This is because the triangular-shaped pool and the room cues were equally reliable as cues for predicting the location of the platform. In this situation associative learning theory (Rescorla & Wagner, 1972) predicts overshadowing should have occurred reciprocally between the room cues and the triangular-shaped shaped pool. That is, the room cues should have restricted learning based on the geometry of the pool and vice versa. Whilst there is certainly no evidence to suggest that the room cues restricted geometric learning there remains a possibility, however slight, that the presence of the triangular-shaped pool may have restricted learning based on the room cues.

Evidence that Group Stable made use of the room cues in addition to the triangular-shaped pool to find the platform is provided by the results of the acquisition phase of the experiment. During this stage Group Stable swam directly to the corner containing the platform significantly more often than Group Rotate (see figure 3.07). In both groups the platform could be found sufficiently well by referring to the shape of the pool. The greater efficiency of Group Stable for finding the platform must therefore be attributable to the presence of the room cues.

Unfortunately, the percentage of time that Group Stable spent searching the correct quadrant of the circular pool during the test with the curtains open did not differ significantly from that exhibited by Group Rotate. This outcome implies that the room cues acquired very little control over Group Stable's behaviour. Thus, evidence that Group Stable referred to the room cues to find the platform is rather mixed. Whilst there is little doubt Group Stable must have used the room cues to find the platform during the training stage, the results of the test in the circular pool are more equivocal. A similar situation arose with Group Stable in the previous experiment. They too exhibited only a weak preference for swimming in the correct quadrant when tested in the circular pool with curtains open, even though they successfully disambiguated the correct from the geometrically equivalent corner during training-presumably by referring to the room cues. Possible explanations for these apparent inconsistencies are discussed below.

One possibility is that the poor performances of Groups Stable during the tests in the circular pool might have resulted from a generalisation decrement caused by removing the boards used to construct the test apparatus. As an alternative, rats may have used the experimental room as a polarising cue to establish North and then headed South-West to find the platform. If this was the case then rats would be expected to learn rather little about the location of the platform relative to the room cues which would then explain the poor performance of rats during the test in the circular pool with the curtains open. Such an account could also explain why Groups Stable found the platform more quickly than Groups Rotate during acquisition. For the latter group, the test apparatus occupied four orientations with respect to the room cues, which presumably made them more difficult to use as a polarising cue and increased escape latencies. A final possibility is that the rectangular and triangular-shaped pools might have restricted learning to locate the platform with reference to the room cues. Unfortunately Experiments 5a and 5b cannot be used to assess fully the latter claim because neither experiment included a control group trained to find the platform with reference to the room cues alone. The next experiment was designed to address this issue.

Before leaving the present discussion it is perhaps worth reconsidering why, in the previous two experiments, Groups Rotate took consistently longer, over the course of training, to find the platform than the experimental groups. One explanation for this effect was mentioned above. Another possibility is that rats may have occasionally swum to the area of the pool where the platform was located on the previous trial, thereby lengthening escape latencies. Had rats approached the platform's previous location on every trial, however, then the room cues would have acquired considerable control over their behaviour. The results of the test in the circular pool with the curtains open would suggest otherwise. Moreover, training procedures were adopted to minimise such behaviour: the pools, for instance, were rotated either clockwise or anticlockwise among the four cardinal points of the experimental room. It also is worth bearing in mind that it was not possible for rats, on any trial, to swim to the area of the rectangular pool previously occupied by the platform- the walls of that environment prevented them from doing so. It thus seems unlikely that any tendency rats had for approaching the platform's previous location first could fully explain the longer escape latencies of Groups Rotate in the previous two experiments.

3.03. Experiment 6

The results of the first two experiments make clear that learning based on shape of the rectangular and triangular-shaped shaped pools was unaffected by the presence of the room cues. Another finding in common with those experiments was that subjects trained to find the platform with reference to the room cues and the shape of the pool exhibited, at best, only a weak preference for searching in the correct quadrant of the circular pool during the test with the curtains open. The latter results occurred despite sufficient evidence to show that the room cues acquired at least some control over searching for the platform during acquisition. This finding is consistent with the conclusion that learning based on the room cues was to some extent restricted by geometric cues.

As already noted, however, neither Experiment 5a nor 5b included a control group, trained to the find the platform with reference to the room cues alone. It is therefore difficult to assess fully the degree to which learning based on the room cues was influenced by the presence of either the rectangular or triangular-shaped shaped pools in the previous experiments.

The primary purpose of the current experiment was to assess whether learning based on the room cues in the previous experiments was restricted by the distinctive shape of the test apparatus. To this end, three groups of rats were trained to find a submerged platform located in one corner of the triangular-shaped pool used during Experiment 5b. A summary of the design and apparatus used for the present experiment is given in figure 3.09. Groups Stable and Rotate were treated identically to their namesakes of the previous experiment. Thus for Group Stable, because the triangle remained in the same orientation with respect to the room cues, escape from the pool was possible by referring to the shape of the pool as well as the cues in the room surrounding it. In contrast, Group Rotate was trained with the triangular-shaped pool in a different orientation for each trial which ensured the triangular-shaped pool rather than the room cues was useful for finding the platform.

The third group, Group Oscillate was novel to this experiment and was trained with the triangular-shaped pool in two orientations with respect to the room cues. These orientations were selected so that the platform remained in the same place relative to the room cues throughout training. However, for some trials the platform was located in one corner at the base of the triangle whilst on others it was in the opposite corner. Group Oscillate could thus find the platform efficiently by referring to the room cues rather than the triangular-shaped pool.

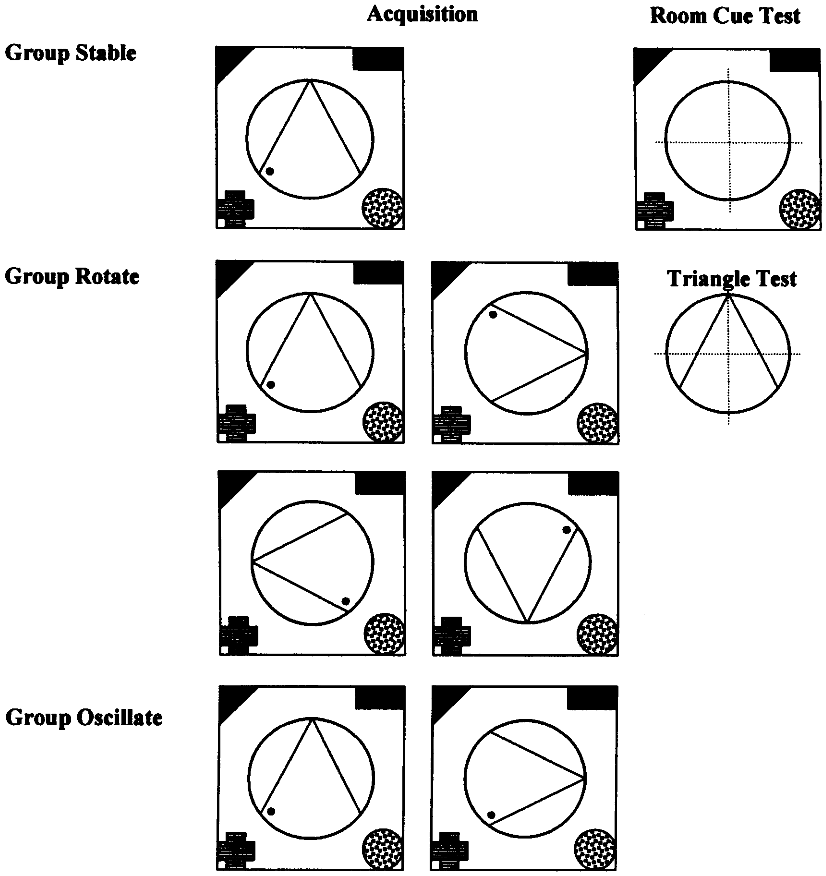

Figure 3.09. Summary of the apparatus and design adopted for Experiment 6. The filled circle represents the platform whist the geometric shapes in the corners of the large square represent the cues of the experimental room.

Contrary to predictions that can be derived from associative learning theory and if there is any generality to the effects described in the previous experiments; then the room cues might not be expected to influence learning based on the triangular-shaped pool in Group Stable. To test this prediction subjects received a test trial in which they were placed in the triangular-shaped pool with the platform removed and with the curtains closed. Evidence that learning based on the shape of the pool had progressed normally would be revealed by Group Stable showing a substantial preference for searching in the quadrant of the pool where the platform was previously located. The performance of Group Rotate during this test would then provide an indication of whether or not the room cues had restricted learning based on the triangular-shaped pool in Group Stable.

Following three further sessions of training with the triangular-shaped pool, subjects were given an additional test undertaken in the circular pool with the curtains open but without the platform. The reason for conducting this test was to examine to what degree, if any, learning based on the room cues in Group Stable had been restricted by the presence of the rectangular arena. Should overshadowing of the room cues by the rectangular pool prove to be successful, then Group Oscillate might be expected to spend considerably more time than Group Stable searching in the area of the circular pool previously occupied by the platform. If on the other hand the triangular-shaped pool should fail to overshadow learning based on the room cues then Groups Stable and Oscillate would be expected to spend approximately the same amount of time searching in the quadrant of the pool previously occupied by the platform during the test.

Method

Subjects and Apparatus The 30 rats were of the same stock, with similar experience, of approximately the same age and housed in the same conditions as those from the previous experiments. At the start of the experiment the rats were assigned randomly to three groups of equal number. The triangular-shaped arena and details of the experimental room were identical to the previous experiment.

Procedure The three groups received 4 trials in each of the 16 sessions of training and were required to escape from a triangular-shaped pool by swimming to a single platform that was always located in one corner at the base of the triangle. Throughout the experiment the curtain remained open. The method used for positioning the platform was the same as that used in the previous experiment. Groups Rotate and Stable were trained identically to their namesake of Experiment 5b. For the third group, Group Oscillate, the platform remained in the same place throughout training but the triangle was moved between two orientations with respect to the room cues. For half the subjects the apex of the triangle was pointed twice in each session towards North and East in relation to the experimental room, whilst for the remaining rats the triangle's apex pointed twice in each session to North and West. As a consequence the platform was located in the left-hand corner at the base of the triangle for half of the trials and for the remaining trials it was located in the right-hand corner at the base of the triangle. The triangle was moved between the two orientations from trial to trial in a random sequence. In addition the sequence with which the triangle was moved varied randomly between sessions. All other procedural details for the acquisition period of the experiment that have been omitted were identical to that of Experiment 5b.

In session 12 there were four training trials and a single test trial. The training trials were conducted in a similar manner to all other acquisition trials. During the test the triangle was positioned so that its apex pointed South in relation to the experimental room and the curtains surrounded the pool. Groups Stable and Rotate were regarded as swimming in the correct quadrant of the pool whenever they entered the quadrant previously occupied by the platform. For a randomly selected half of Group

Oscillate the correct and incorrect quadrants of the pool were the North-East and North-West quadrants respectively, whilst for the remaining subjects the significance of these quadrants was reversed. All other procedural details for the test that have been omitted were identical to those of the previous experiment.

Following the test in the triangular-shaped pool with the curtains closed rats received three further sessions of training. These trials were identical to all other training trials as were the first four trials of session 16. On the fifth test-trial the boards that the triangle was constructed from were removed from the pool as was the platform and the curtain remained open. For the purpose of the test the pool was divided along its North-South and East-West axes into four quadrants of equal area. Groups Stable and Oscillate were regarded as swimming in the correct region of the pool whenever they entered the quadrant previously occupied by the platform. For these groups the incorrect quadrant was the one to the right of and adjacent to the one just described. For a randomly selected half of Group Rotate the correct and incorrect quadrants were the South-West and South-East quadrants respectively, whilst for remaining rats the significance of these quadrants was reversed. All other procedural details for the test with the circular pool that have been omitted were identical to that of previous experiment.

Results and Discussion

The group mean escape latencies for acquisition trials that took place in the triangle-shaped pool during the first 16 sessions of the experiment can be seen in figure 3.10. Generally all three groups showed a decrease in their escape latencies as the sessions progressed. However, Group Stable was quicker to escape onto the platform than the other two groups and this result suggests that Group Stable made use of the room cues as well as the shape of the pool to find the platform. Another observation worth some comment is that Groups Rotate and Oscillate took approximately the same amount of time to find the platform, which implies that the triangular-shaped shaped pool and the room cues were of equal salience.

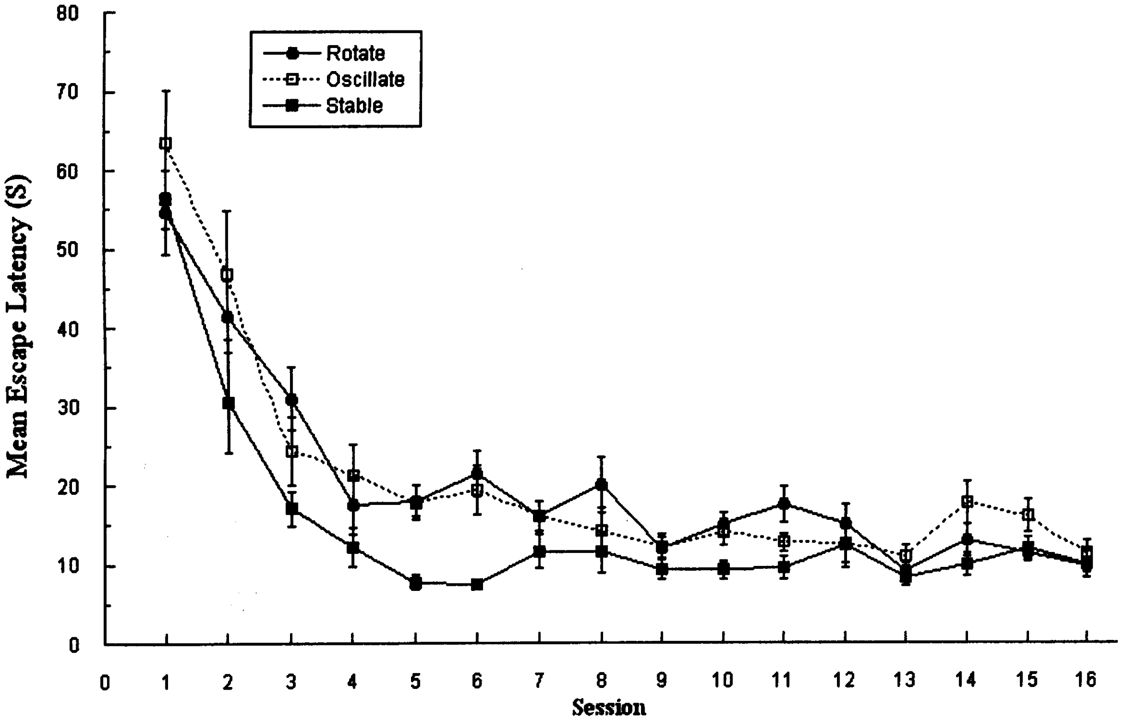

Figure 3.10. Mean escape latencies for the three groups during acquisition trials that took place with the triangular-shaped pool and with the room cues over the 16 sessions of training (error bars indicate +/-1 standard error).

To assess these trends more formally, a mixed two-way ANOVA of escape latencies over the 16 sessions for the three groups, showed a main effect of group, F(2, 27)=13.84, Mse= 128.04, p= 0.00, η_p^2= 0.51, and of session, F(15, 405)=57.1, Mse= 85.41, p= 0.00, η_p^2= 0.68, but the interaction of Group x Session was not significant, F(30, 405)=1.22, Mse= 85.41, p= 0.20, η_p^2= 0.08. Further comparisons using the Sheffé procedure revealed that Groups Rotate and Oscillate did not differ in the amount of time they took to find the platform, F(1, 27)= 0.19, Mse= 128.04, p= 0.05, η_p^2= 0.01. Given that the shape of the pool and the room cues were equally reliable for finding the platform the latter results suggest that the salience of these cues was rather similar. Comparisons also revealed that Group Stable was significantly quicker to escape from the pool than either of the other two groups, F(1, 27)=27.50, Mse= 128.04, p<0.00, η_p^2= 0.50.

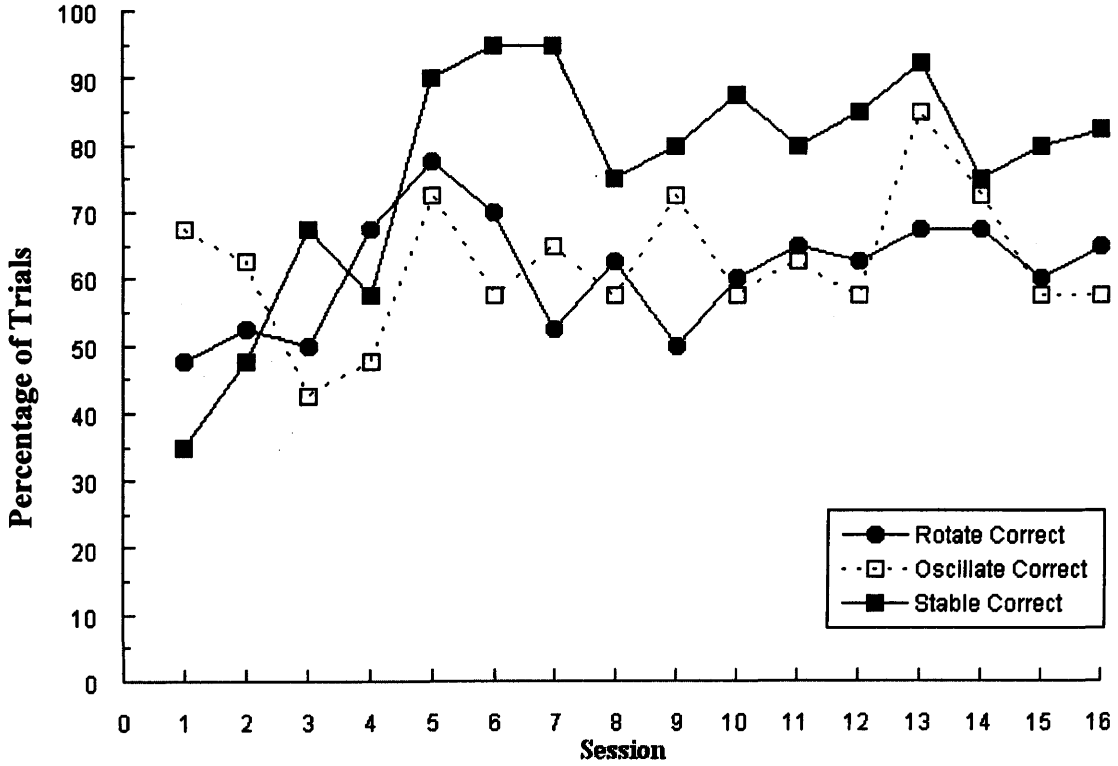

Figure 3.11. Mean percentage of trials that the groups first entered the correct corner of the triangular-shaped pool for the each of the 16 sessions of training.

The mean percentages of trials on which subjects swam directly to the correct corner during training are shown for the three groups in figure 3.11. Training was more successful with Group Stable than for the other two groups and this result once again suggests that Group Stable made use of room cues in addition to the shape of the pool to find the platform. Moreover, the results of Group Rotate, for which the shape of the pool was relevant for finding the platform, were very similar to the results of Group Oscillate, for which the room cues were relevant for finding the platform. Once more this observation suggests that there was very little difference between the salience of room cues and the shape of the pool. Comparisons of individual mean percentages of trials on which the correct corner was entered first for the 16 sessions combined revealed a significant difference between Group Stable and each of Groups Rotate and Oscillate, Us(10, 10)≤22, but the difference between the latter two groups was not significant, U(10, 10)=55.

The mean percentages of trials on which the corner of the pool where the platform was located, the opposite corner and the apex respectively, were entered first for the 16 sessions combined were: 77, 17 and 6 for Group Stable; 61, 28 and 11 for Group Rotate; and 62, 29, and 9 for Group Oscillate. Between group comparisons revealed that Group Stable made significantly fewer errors of searching the opposite corner than each of the other two other groups Us(10, 10)=12. Groups Rotate and Oscillate entered first the opposite corner equally often U(10, 10)=51. These comparisons show that on some trials the latter two groups entered first the opposite corner before finding the platform in the correct corner. The implications of these results shall be reserved until the general discussion of the chapter.

Paired comparisons revealed that for each group the correct corner was entered first significantly more often than either the opposite corner or the apex, Ts (10)≤2. These findings confirm that each group discriminated the corner containing the platform from the other two corners of the pool. This discrimination must have therefore been based on the shape of the pool in Group Rotate and on the room cues in Group Oscillate whilst Group Stable could have used either cue, or both.

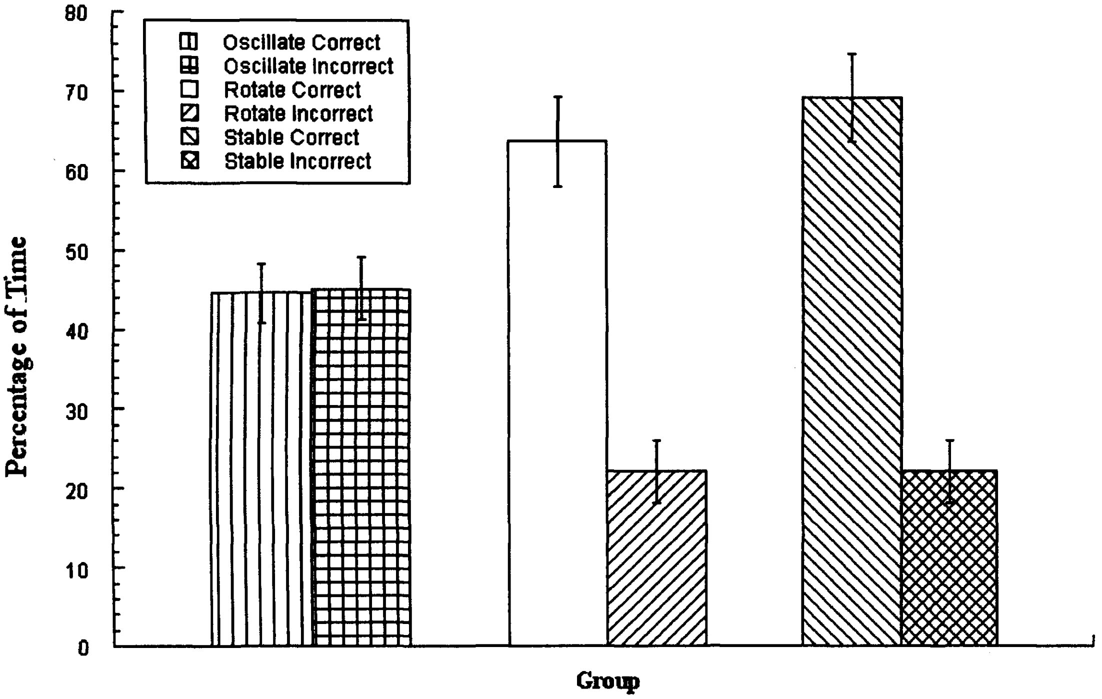

Figure 3.12. Mean percentage of time the groups spent searching in the correct and incorrect quadrants of the triangular-shaped pool during the 60-s test trial (error bars indicate+/- 1 standard error).

The mean percentages of time spent in the correct and incorrect quadrants of the triangular-shaped pool during the 60 s test trial with the curtains closed are illustrated in figure 3.12 above. The figure shows that Groups Rotate and Stable spent more time searching in the correct than the incorrect quadrant of the pool, but Group Oscillate did not show a preference for either quadrant. A two-way ANOVA of the groups and of the time spent in the correct and incorrect quadrants of the pool showed a significant main effect of quadrant, $\underline{F}(1, 27)=47.28$, Mse= 291.06, $\underline{p}= 0.00$, $\eta_p^2=0.64$, and a significant interaction of Group x Quadrant, $\underline{F}(2, 27)=12.62$, Mse=291.06, $\underline{p}=0.00$, $\eta_p^2=0.48$, but the main effect of group was not significant $\underline{F}(2, 27)= 0.35$, Mse= 57.72, $\underline{p}= 0.71$, $\eta_p^2= 0.03$. Simple effects tests revealed that Group Stable spent significantly more time in the correct than the incorrect quadrant of the pool, $\underline{F}(1, 27)=42.76$, Mse= 291.06, $\underline{p}=0.00$, $\eta_p^2= 0.61$, as did Group Rotate, $\underline{F}(1, 27)= 29.76$, Mse= 291.06, $\underline{p}= 0.00$, $\eta_p^2= 0.52$, but Group Oscillate failed to show a preference $\underline{F}(1, 27)= 0.01$, Mse= 291.06, $\underline{p}= 0.934$, $\eta_p^2= 0.00$. Further tests of simple effects revealed a significant difference between the groups in the percentage of time they searched in the correct quadrant, $\underline{F}(2, 254)= 9.7$, Mse= 174.39, $\underline{p}= 0.00$, $\eta_p^2= 0.18$. Additional tests using the Sheffé procedure showed that Groups Stable and Rotate who did not differ, ($\underline{F}(1,54)= 0.89$, Mse= 174.53, $\underline{p}= 0.77$, $\eta_p^2= 0.02$) spent more time in the correct quadrant of the pool than Group Oscillate, $\underline{F}(1,54)= 18.11$, Mse= 174.53, $\underline{p}<0.00$, $\eta_p^2= 0.25$. These analyses confirm that for Group Stable learning based on the shape of the pool was not restricted by the presence of the room cues.

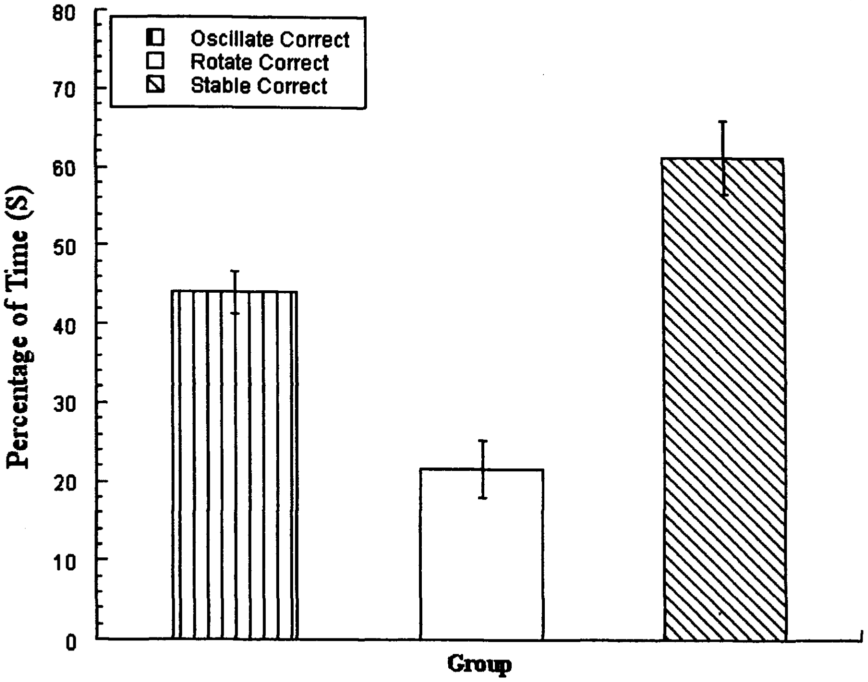

Figure 3.13. Mean percentage of time the groups spent searching in the correct quadrant during the 60 s test trial in the circular pool with the curtains open (error bars indicate+/- 1 standard error).

The mean percentages of time spent in the correct quadrant of the pool during the 60 s test conducted in the circular pool with the curtains open and are shown in figure 3.13. The results of the test show that unlike Group Rotate, Groups Stable and Oscillate spent a considerable amount of time searching in the quadrant of the pool where the platform was originally located. One sample t-tests revealed that Groups Stable, t(9)= 7.73, p= 0.00, and Oscillate, t(9)=7.33, p= 0.00, spent more than 25% of their time searching in the correct region of the pool, but for Group Rotate this figure was below 25%, t(9)= -0.93, p= 0.38. A one-way ANOVA of the percentages of time that the groups spent searching in the correct quadrant of the pool showed a significant main effect of group, F(2, 27)=28.48, Mse= 140.4, p=0.00, η_p^2=0.68. Subsequent comparisons using the Sheffé procedure revealed that Group Stable spent significantly more time in the correct quadrant than either Groups Rotate, F(1, 27)=56.69, Mse= 140.41, p= 0.00, η_p^2=0.68, or Oscillate, F(1, 27)=10.99, Mse=

140.41, p=0.00, η_p^2=0.29. The latter result is perhaps somewhat surprising because it suggests that the presence of the triangular-shaped pool potentiated rather than overshadowed learning based on the room cues in Group Stable. Finally, Group Oscillate spent more time searching the correct quadrant of the circular pool than Group Rotate, F(1, 27)=17.76, Mse=140.41, p=0.00, η_p^2=0.40, which confirms that the room cues acquired control over the behaviour of the former group.

Unlike the previous two experiments, the results of the test conducted in the circular pool showed that Group Stable spent a considerable amount of time searching in the quadrant previously occupied by the platform. Similar procedures were used for training and testing during all three experiments which makes it difficult to explain the disparity between the results. As noted earlier, it is possible that the poor spatial learning based on the room cues exhibited by the Groups Stable in Experiments 5a and 5b resulted from a generalisation decrement caused by removing the boards used to construct the rectangular and triangular-shaped pools. Why this should have occurred in the first two experiments and not the current one is uncertain.

Together the results of both test trials show that there was no hint of cue competition. During the first test Group Stable showed a preference for swimming in the correct quadrant of the triangular-shaped pool that was almost as strong as that exhibited by Group Rotate. There was thus no indication that the room cues prevented Group Stable from learning to locate the platform with reference to the shape of the pool. In addition, Group Stable spent more time than Group Oscillate searching the correct quadrant of the circular pool during the second test. Not only does this result suggest that cue competition failed but it also implies that the triangular-shaped pool facilitated, or potentiated learning based on the room cues in Group Stable. Possible mechanisms for the latter effect shall be taken up in the general discussion of this chapter and explored further in the next.

The present results are consistent with the idea that the triangular-shaped pool did not overshadow and was not overshadowed by learning based on the room cues. They are thus incompatible with associative learning theories like the Rescorla-Wagner (1972). If, however, room cues can be likened to landmarks, then the present results are not only consistent with the ideas expressed in the theory of the Geometric Module (Cheng, 1986; Gallistel, 1990) but they also extend the circumstances in which the failures to detect cue competition between featural and geometric cues occur.

3.04. General Discussion

The original reason for conducting these experiments was to test whether cues located outside an environment might restrict learning based on its shape. Not one study to date, until now, has been designed to address this issue directly. Margules and Gallistel (1988) have shown that room cues can control searching for a goal hidden in one corner of a rectangular arena; but their study included neither the appropriate tests nor control group to test for the effects of cue competition. All the previous studies were designed to address these concerns, but not one of them revealed any evidence of cue competition. The results of the first two experiments showed that the room cues failed to overshadow learning based on the rectangular and triangular-shaped pools. In the final experiment the absence of cue competition was reciprocal: learning based on the triangular-shaped pool neither overshadowed nor was overshadowed by the presence of the room cues. These results are thus incompatible with associative learning theories (Mackintosh, 1975; Pearce & Hall, 1980; Rescorla & Wagner, 1972).

One way to reconcile the present results with the aforementioned theories is to assume that the room cues were of relatively low salience compared to shape of the pool, making them ineffective as a cue for overshadowing. Fortunately the results from the training stage of Experiment 6 can be used to show that there was very little difference between salience of the room cues and, at least, the triangular-shaped pool. In that study Groups Rotate and Oscillate not only took the same amount of time to escape from the pool, but they also entered first the corner with the platform equally often. This similarity in performance occurred even though Group Rotate had to find the platform with reference to the triangular-shaped pool and Group Oscillate had to use the room cues. Given that these cues were equally reliable for finding the platform, then the logical conclusion to draw from the experiment is that they were of similar salience. The same experiment also revealed a reciprocal absence of overshadowing, which again reinforces the idea that there was no difference between the salience of the room cues and the triangular-shaped pool. It thus seems unlikely that the absences of cue competition observed in the final two experiments resulted from the room cues being less salient than the triangular-shaped pool.

Unfortunately, it is difficult to assess stimulus salience in the first study because for the experimental group, the room cues were more reliable than the rectangular pool for finding the platform. Even so, according to the Rescorla-Wagner model (1972) these conditions should have restricted the degree of learning based on the shape of the pool more than on the room cues, making the latter more effective as a cue for overshadowing. The first experiment, however, provided no hint that the room cues had prevented Group Stable from learning to locate the platform with reference to the shape of the pool. This absence of cue competition is thus more striking than the failures of the room cues to overshadow learning based on the triangular-shaped pools.

Despite the repeated failures to find cue competition it is possible that the room cues were for some other reason a poor cue for overshadowing. One possibility is that the boards used to create arenas occluded the room cues which prevented rats from viewing them as they swam around the pool. Fortunately the experiments provide evidence to the contrary. Reconsider Group Stable, who in the first experiment, was trained to find the platform hidden in one corner of the rectangular pool. Even though the pool itself was devoid of features rats reliably disambiguated the correct from the geometrically equivalent corner. They must have therefore referred to cues outside the rectangular pool: those provided by the experimental room, to do so. The results from the final experiment also make clear that rats could see the room cues from the triangular-shaped pool. In that study, Group Oscillate learned to locate the platform with reference to the room cues even though it occupied one of the two corners at the base of the triangular-shaped pool throughout training.

It is also worth pointing out that other studies, conducted in the same laboratory as my own experiments have shown that room cues can overshadow and block spatial learning based on an intramaze landmark (Roberts & Pearce, 1998; 1999). It thus appears that in some circumstances, at least, the room cues used in the previous experiments can influence spatial learning. It is therefore unreasonable to attribute the absence of overshadowing found in any of the previous experiments to some inherent property of the room cues that rendered them unsuitable for revealing the effects of cue competition.

One conspicuous and interesting finding from the final experiment is that Group Stable spent more time than Group Oscillate searching the correct quadrant of the circular pool during the test with the curtains open. For Group Stable the triangular-shaped pool and the room cues were relevant for finding the platform but for Group Oscillate only the room cues were relevant. It thus appears that the triangular-shaped pool facilitated, rather than overshadowed, learning to locate the platform with reference to the room cues in Group Stable.

There are several ways to explain why Group Stable may have learned more about the position of the platform relative to the room cues than Group Oscillate. First, it is possible that this facilitation or potentiation effect might have resulted from the occurrence of between-stimulus associations. In Group Stable, for instance, the room cues and the triangular-shaped pool might have become associated with the platform, whilst simultaneously becoming associated with each other during acquisition. On being released into the circular pool for the test with the room cues, rats may have headed towards the correct quadrant of the pool guided initially by the room cue-platform association. It is likely that swimming in the correct quadrant would evoke the memory for the triangular-shaped pool and its conditioned properties by virtue of the association that developed between the shape of the pool and the room cues during training: encouraging rats to spend even more time in the correct quadrant. It is unlikely that between-stimulus associations would have a similar influence in the other two groups, primarily because for them only one cue could be used to find the platform. Consequently during the test with the circular pool Group Oscillate might have been chiefly guided by the room cue-platform association whilst for Group Rotate guidance would have been provided by the triangle-platform association. Because of this difference between the groups, Group Stable would have exhibited a greater preference compared to the other two groups, for swimming in the correct quadrant of the pool.

If between-stimulus associations were responsible for the observed potentiation effect then the circumstances in which they formed were remarkable. Even though the conditions used to train Group Stable were theoretically sufficient to permit the occurrence of between-stimulus associations, the room cues were nevertheless some distance away from the triangular-shaped pool. Other experiments that have purported to reveal the effects of between-stimulus associations have used stimuli that were presented much closer together in time and space: simultaneous presentation of a taste and odour in solution for example (Speers Gillan, & Rescorla, 1980). Whether it is appropriate to attribute the potentiation in Experiment 6 to the development of between-stimulus associations remains uncertain because the stimuli that study differed in nature from more traditional conditioning experiments (see Durlach & Rescorla, 1980; Speers et al, 1980; Rusiniak, Hankins, Garcia & Brett, 1979).

Bouton, Dunlap and Swartzentruber (1987) have shown that one factor known to influence potentiation is relative stimulus salience. They gave subjects compounds of two flavours and observed potentiation only when the salience of the target flavour was weak and the one accompanying it was of an intermediate salience. The results of the final experiment have already been interpreted as showing that there was no difference between the salience of the triangular-shaped pool and the room cues. According to Bouton et al (1987) such conditions are not conducive to observe potentiation, which makes its occurrence in Experiment 6 rather surprising. Further discussion regarding between-stimulus associations and the salience of the target stimulus shall be reserved until the following chapter.

Another way in which to explain the potentiation-type effect is to appeal to the habit strength that the groups may have acquired for swimming to a particular region of the pool (see Hayward et al, 2003). During acquisition rats of Group Stable were more likely to swim directly to the platform than Group Oscillate because there were two cues for identifying the platform's position rather than one. Thus, the training given to Group Stable might have resulted in them acquiring a stronger habit of swimming to a particular region of the pool, by reference to the room cues, than Group Oscillate. The transfer of these different habit strengths to the test trial would then account for the stronger preference for the correct quadrant shown by Group Stable than by Group Oscillate.

As an alternative explanation, Group Oscillate may have developed a strategy which interfered with their learning to locate the platform with reference to the room cues. During training, for example, this group swam first to the opposite corner at the base of the triangular-shaped pool more often than Group Stable. Group Oscillate must have therefore occasionally swum first to the opposite corner at the base of the triangle before then heading toward the corner containing the platform. Such a strategy would impede learning to find the platform with reference to the room cues because it would encourage rats to search an area of the pool without the platform.

There were few occasions when Group Stable searched the opposite corner at the base of the triangle; making it unlikely they developed a similar strategy habit of swimming to the opposite corner first. The training given to Group Oscillate may have therefore, inadvertently, resulted in them acquiring a stronger habit, compared to Group Stable of swimming to the opposite first. Transfer of these habit-strengths would then explain why Group Oscillate showed a weaker preference than for Group Stable searching the correct region during the test in the circular pool with the curtains open.

Even if Group Oscillate had developed a habit of swimming to the opposite corner first; the results of a study conducted by Graham, Good, McGregor and Pearce (2006) imply that such a habit would have had little impact on learning to locate the platform with reference to the room cues. In one experiment, rats were trained to find a submerged platform that always occupied the same right-angled corner of a kite-shaped a pool: the correct corner. For Group Shape Only, the correct corner had black walls for half the trials and white walls for the other half. The shape of the pool was thus relevant for finding the platform whilst the colour of the walls was irrelevant. For Group Shape and Colour, the correct corner always had black walls, making wall colour and shape relevant for finding the platform. After successful completion of the training stage rats were given a test trial in an entirely black kite-shaped pool without the platform. Surprisingly the results of the test showed that Group Shape and Colour showed a greater preference for the correct corner than Group Shape Only who in turn failed to show any preference for either right-angled corner of the kite.

Graham et al (2006) noted that during training Group Shape Only made fewer correct choices when the corner with the platform was white than when it was black. These rats may have therefore developed a habit of swimming toward the black corner which interfered with their learning to locate the platform with reference to the shape of the pool. In an effort to limit the effects of this strategy Graham et al (2006) repeated the above experiment with the same groups, but above the platform was placed a beacon which they anticipated would diminish the tendency that Group Shape Only had for approaching the black corner first. The results from the training stage confirmed this manipulation proved successful. After training rats were given a test trial in the kite-shaped pool without the platform, as before. The test replicated the findings above: Group Shape and Colour showed a substantially greater preference for the correct quadrant than the Group Shape Only. The presence of the beacon during training, even though it successfully reduced the habits acquired by Group Shape Only, had little impact on conditioning with the kite.

The results of Graham et al (2006) thus suggest that effects of habits on spatial learning based on the shape of a test arena appear to be rather weak. If their influence is similarly weak on spatial learning based upon room cues; then it is unreasonable to argue that the poor performance of Group Oscillate during the test in the circular pool with the curtains open resulted from rats developing a habit which interfered with learning based on the room cues. Such conclusions, however, need to be taken with a measure of caution because it relies on extrapolations drawn from several experiments. Even so, if there is any merit, at all, to these ideas then it would strengthen the conclusion that learning based on the room cues in Group Stable was potentiated by the triangular-shaped pool.

In contrast to many other studies showing that cues outside a maze can restrict learning based on those located inside (Chamizo et al, 1985; March et al, 1992; Roberts & Pearce, 1998); the present results show for the first time that the presence of room cues do not overshadow and are not overshadowed by learning based on the shape of an test arena. Such results are not only perfectly consistent with the failures of an intramaze landmark to restrict spatial learning based on the shape of a swimming pool found in Chapter 2; they also extend the conditions under which the failures to find cue competition between featural geometric cues occur. These results are thus largely consistent with the theory of the Geometric Module (Cheng, 1986; Gallistel, 1990), which postulates that geometric and featural information are processed by independent modules.

If these modules are independent, however, it becomes difficult to understand just how the triangular-shaped pool could have potentiated learning based on the room cues in the final experiment. In contrast to the proposals of Cheng (1986) and Gallistel (1990), Newcombe (2002; see also Cheng & Newcombe, 2005) has suggested that geometric information is integrated with other types of information (like landmarks) into a single representation of the environment. If there is any merit to this claim then it would provide one way in which the training given to Group Stable could have resulted in them learning more about the position of the platform, relative to the room cues than Group Oscillate. Unfortunately, the manner in which Newcombe (2002) presents this idea is rather ambiguous, making it difficult to be precise about any predictions based upon it. What is certain, though, is that in its original form the Geometric Module theory (Cheng, 1986; Gallistel, 1990) offers an incomplete account of spatial learning based on the shape of an environment.

Chapter 4.

Potentiation of Learning based on a Rectangular Pool by a Landmark, but a Failure to Find Evidence of Between-Stimulus Associations.

So far it has been assumed that overshadowing will always occur when animals are conditioned with two stimuli presented in compound (Kamin, 1969; Pavlov, 1927). Durlach and Rescorla (1980) have, however, shown that in some circumstances animals will learn more about one stimulus when it is presented in compound with another, than if it is separately paired with the same unconditioned stimulus (US). In one experiment Durlach and Rescorla (1980) gave an aversive stimulus to rats subsequent to them drinking solutions with an odour alone, or a different odour and taste. Tests, during which rats were given simultaneous access to solutions of each odour, revealed that conditioned aversion was stronger to the odour presented in compound with taste than to the odour presented alone. The presence of taste thus appears to have facilitated or potentiated learning based on the odour rather than overshadowing it (see Speers et al, 1980; Rusiniak et al, 1979, for similar results).

Effects similar to those described above have also been observed in spatial learning experiments. In the study conducted by Graham et al (2006) mentioned earlier, rats were trained to find a submerged platform that occupied one right-angled corner of a kite-shaped pool: the correct corner. For the experimental group the correct corner had black walls and the other right-angled corner had white walls which ensured the shape of the pool and wall-colour were relevant for finding the platform. When tested in an entirely black kite without the platform, the experimental group showed a greater preference for the correct corner than a control group for which only the shape of the pool was relevant for finding the platform. The black walls thus seem to have potentiated spatial learning based on the kite in the experimental group.

Another experiment to reveal evidence of potentiation in spatial learning was conducted by Pearce et al (2001) who trained an experimental group of rats, Group Beacon, to find a submerged platform located in one corner at the base of a triangular-shaped pool: the correct corner. The platform could be found by heading toward a landmark that was fixed to it or by referring to the geometry of the pool. The control group, Group Two, was treated identically except an additional landmark, identical to the first, was placed in the corner diametrically opposite to the correct corner. For these rats the landmark was thus irrelevant for finding the platform whilst the geometry of the pool was relevant.

Following sufficient training, the groups were given a test trial conducted in the triangular-shaped pool without platform and landmarks, the results of which revealed that Group Beacon spent considerably more time than Group Two searching in the correct corner. There was thus an indication that spatial learning based on the correct corner was potentiated by the landmark in Group Beacon.

To explore further the above possibility Pearce et al (2001) gave the groups reversal training during which the submerged platform, without the landmark attached to it, was placed in the corner at the base triangle diametrically opposite to that containing the platform during training. Pearce et al (2001) reasoned that if the landmark potentiated spatial learning based on the correct corner in Group Beacon, they should be slower to learn the about the new location of the platform than the other group.

The results confirmed this prediction which provides further evidence to suggest that the landmark potentiated learning based on the triangular-shaped pool.

The results of Experiment 6 provide a rather different example of potentiation. In that study rats were trained to find a submerged platform in one corner of a triangular-shaped pool, surrounded by room cues. When tested in the circular pool with the curtains open, evidence of spatial learning based on the room cues was greater in Group Stable than for Group Oscillate. For the former, the shape of the pool and the room cues were relevant for finding the platform whilst for the latter only the room cues were relevant. Learning based on the room cues thus appears to have been potentiated by the triangular-shaped pool in Group Stable (see Hayward, et al 2003).

The results described in Chapter 2 also hint at the possibility that learning based on the shape of an environment may have been potentiated by the presence of the landmark. In Experiment 1, for instance, Group Landmark was trained to find a submerged platform located in the same corner of a rectangular pool as a spherical landmark. During a test trial without the platform and landmark, rats showed a numerically greater preference for the geometrically correct quadrants than a control group which was trained in the absence of the landmark. Learning based on the rectangular pool seems to have been potentiated, to some degree, by the presence of the landmark in the experimental group. It is perhaps worth pointing out that similar trends were observed in the majority of the experiments included in Chapter 2, except the third. Thus, experimental groups for which the shape of the pool and a landmark were relevant for finding a platform always exhibited a numerically greater preference for searching the geometrically correct corners than the relevant control groups. Such results occurred with triangular-shaped pool in Experiment 2 and when four identical landmarks described a rectangle in Experiment 4.

As noted in the previous chapter, one factor known to influence potentiation is relative stimulus salience. Bouton et al (1987) observed potentiation when the salience of the target stimulus was weak relative to the one accompanying it. If this proposal is correct, then it would have to be assumed that the target stimuli in all the aforementioned studies were of relatively low salience. Unfortunately, the relationship between stimulus salience and potentiation in spatial learning is far from clear. The study conducted by Graham et al (2006), mentioned earlier, found evidence of potentiation and showed the kite to be less salient than the black walls; a result which is entirely consistent with Bouton et al's (1987) proposal. In a related study Pearce, Graham, Good, Jones and McGregor (2006) have shown that the same cue can overshadow learning based on a rectangular pool. They trained an experimental group of rats to find a platform that was hidden in the corner of the rectangular pool where two black walls, one long the other short, met. Rats could thus find the platform by referring to the shape of the pool or the coloured walls. The platform had a landmark attached to it which, based on the results of Pearce et al (2001) and Hayward et al (2003; Hayward, Good & Pearce, 2004), was not expected to influence the outcome of the experiment. Tests, without the platform and landmark, were executed in a rectangular pool which had four white walls. During the test the experimental group displayed a weaker preference for the corner previous occupied by platform (and the geometrically equivalent corner) than a control trained in an all-white arena, which implies that learning based on the rectangle was restricted by the black walls. To account for this finding Pearce et al (2006) argued that the black walls must have been more salient than rectangular pool, but failed to provide any firm evidence to substantiate this claim.

Experiments 2, 3 and 4 showed the landmark to be more salient than environmental geometry, conditions which according to Bouton et al (1987) should have resulted in learning based on the latter cue becoming potentiated. There was a hint of potentiation in those studies, but the effect was not significant. By comparison Experiment 6 showed that learning based on the room cues was potentiated by the triangular-shaped pool, even though there was no difference between the salience of these cues: a finding which is difficult to reconcile with Bouton et al's (1987) ideas.

Despite the above controversies, it is clear that potentiation rather than overshadowing can sometimes occur when animals are conditioned with two stimuli presented in compound (Rescorla & Durlach, 1980). The results supplied by Pearce et al (2001) and Graham et al (2006) suggest that the presence of an intramaze landmark can potentiate learning based on the distinctive shape of a swimming pool. Similar trends were observed in the majority of studies included in Chapter 2. A rather different effect was found in Experiment 6, which revealed that a triangular-shaped pool potentiated learning based on the cues supplied by an experimental room. Potentiation-type effects in spatial learning thus seem to be both reliable and general. The question is then raised how might these effects be explained?

One explanation is that potentiation arises from the development of between-stimulus associations (Rescorla, 1981). Another possibility is that one element present in a compound stimulus may enhance the association between the US and the remaining element of the compound, but this explanation is nothing more than a description of the results. One study that can be used to distinguish between these explanations for potentiation was conducted by Speers et al (1980). They gave rats two pairs of compound flavours: sucrose and hydrochloric acid (SH) and salt and quinine (NQ), followed by a mild aversive stimulus. Subsequently one element, H, was followed by a strong aversive stimulus and one element, Q, was extinguished. Results of a test trial, during which subjects were given simultaneous access to S and N, showed that rats rejected S in favour of N. To explain this outcome Speers et al (1980) argued that S was rejected because it borrowed the conditioned aversion of H by virtue of the between-stimulus association that formed during compound presentation of S and H in the first stage. Similarly, despite a between-stimulus association developing between N and Q during Stage 1 rats failed to reject N because the conditioned aversion of Q was extinguished in Stage 2. It thus becomes difficult to explain potentiation in terms of enhancement of the CS-US association. Indeed without postulating between-stimulus associations it is difficult to explain why the training that took place in Stage 2 should have influenced Stage 1 acquisition.

The experiment conducted by Speers et al (1980) provides evidence to show that between-stimulus associations can develop between two neutral stimuli when they are presented in compound. When such associations occur they seem to have a potentiating effect that counteracts the tendency of one stimulus to overshadow another. There is evidence to suggest that between-stimulus associations can also arise when blocking designs are used (Speers et al, 1980). It therefore seems reasonable to argue that blocking and overshadowing may have occurred in my own experiments with the effects of cue competition being masked by the potentiating influence of between-stimulus associations.

Even so, given that experiments purporting to reveal the effects of between-stimulus associations have typically used stimuli presented in close spatial and temporal proximity (Speers, 1981); it is unlikely that referring to between-stimulus associations could account for the potentiation observed in Experiment 6. For the experimental groups of Chapter 2, however, the landmark always occupied the same corner of the pool as the platform. These conditions ensured that featural and geometric cues were presented close together which may have resulted in the landmark becoming associated with the shape of the pool. According to Speers et al (1981) such associations are likely to potentiate rather than restrict spatial learning based upon the geometry of the pool. If there is any merit to this idea then the repeated failures to find cue competition in Chapter 2 might then be explained in purely associative terms (Rescorla & Wagner, 1972) and the need to postulate a Geometric Module (Cheng, 1986; Gallistel, 1990) would become redundant.

The experiments in this chapter were designed to provide, first, an example of potentiation in a spatial learning and second, to assess whether potentiation might be explained by the development of between-stimulus associations.

4.01. Experiment 7

As noted above the experiment conducted by Pearce et al (2001) provides evidence to suggest that learning based on the shape of an environment was potentiated by the presence of an intramaze landmark. The results of Experiment 1 lend some support to this idea by showing that Group Stable, for which the rectangular pool and landmark were relevant for finding the platform, spent more time searching in the correct quadrants during the test than rats trained without a landmark. Unfortunately the potentiation effect observed in Experiment 1 was not significant. However, there are several ways in which to explain the disparity between the results of Pearce et al (2001) and those of Experiment 1. Pearce et al (2001) used a triangular-shaped pool and a landmark that was attached to the platform. By comparison, Experiment 1 used a rectangular pool and a spherical landmark, located some distance away from platform. Finally, Pearce et al (2001) adopted a reversal training procedure designed to reveal the effects of potentiation. Such training was not undertaken in Experiment 1 and it may be a more sensitive measure to reveal the effects of potentiation than the test conducted in the rectangular pool without the landmark or platform.

In view of the above discussion Experiment 7 was primarily designed to provide evidence to show that learning based on a rectangular pool might be potentiated by the presence of an intramaze landmark. The design of the experiment was similar to that used for Experiment 1 of Chapter 2 with the following exceptions. A vertical rod, attached to the platform and identical to that used by Pearce et al (2001), replaced the spherical landmark used for the earlier experiment. One reason for using this landmark is that Pearce et al (2001) found it to be an effective cue to reveal the effects of potentiation.

The experiment included two groups of rats, trained to find a submerged platform located in one corner of a rectangular pool (see figure 4.01, left-hand column). For the experimental group, Group Landmark, a landmark was attached to the platform. This group could thus use the landmark but not the shape of the pool to unambiguously identify the location of the platform. Accordingly, theories of associative learning (Rescorla & Wagner, 1972) predict that the landmark should restrict the extent to which the shape of the pool is used to find the platform. However, based on previous results the landmark might not be expected to impede learning based on the rectangular pool. Finally, if there is any generality to the results of Pearce et al (2001) or the results of Experiment 6 it is possible that the presence of the landmark will potentiate learning based on the rectangular pool.

A control group, Group Two Landmarks, was trained in the presence of two landmarks. The first was attached to the platform and together these objects occupied the same corner of the pool as they did for Group Landmark. The other landmark, being identical to the first, was located in an adjacent corner but did not have a platform beneath it. As a result the landmark and the shape of the pool individually provided ambiguous information for locating the platform, but together they could be used to find the platform. According to theories of associative learning (Rescorla & Wagner, 1972) the control acquired by the shape of the pool, over searching for the platform, should be greater for Group Two Landmarks than for Group Landmark. To test this prediction a test trial was conducted during which rats were placed in the pool in the absence of the platform and landmarks. The percentage of time spent in the correct quadrants of the pool: the quadrant previously occupied by the platform and its geometric equivalent, was recorded. If there is any evidence that the landmark had overshadowed spatial learning based on the shape of the pool then Group Landmark would be expected to spend less time swimming in the correct quadrants of the pool than the control group.

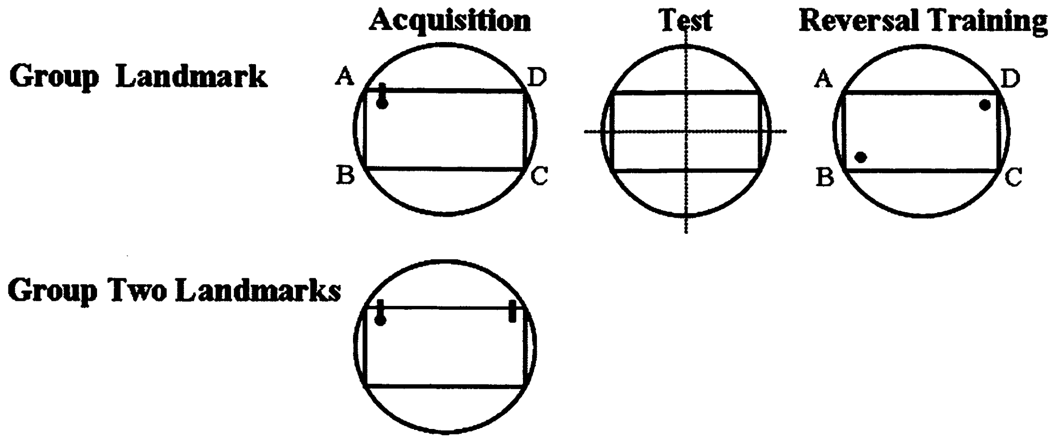

Figure 4.01. The design and apparatus used for Experiment 7. The location of the platform is given by the filled black circle. Short vertical lines indicate the positions of the landmark/s.

Subsequent to the test trial, rats were given reversal training similar to that undertaken by Pearce et al (2001). For this stage of the experiment the landmarks were removed from the pool and the groups were trained with two platforms which occupied geometrically equivalent corners of the pool (see figure 4.01, right-hand column). Importantly the platforms were placed in corners which were different, geometrically, from that occupied by the platform in the previous stage. At the outset of this stage, the control group would be expected to search in the corner originally occupied by the platform, which would interfere with learning about the new locations- slowing their escape from the pool. This tendency to approach the original corner should diminish after a number of trials, shortening escape latencies. If cue competition should fail the performance of Group Landmark during the final stage should match that of the control group. If there was any hint of potentiation then Group Landmark would be slower than the control group to relinquish their tendency to search the corner originally occupied by the platform. As a result they should take longer than the control group to find the platform throughout the final stage.

Method

Subjects The 20 rats were of the same stock, with similar experience, of approximately the same age, and housed in the same conditions as those of the previous experiment. Half of the subjects had previously participated in an appetitive Pavlovian conditioning experiment for which they had been reduced to 80% of their free-feeding weights. They were allowed unrestricted access to food and water for two weeks prior to the start of the present experiment and for the duration of the experiment itself. At the start of the experiment rats were randomly assigned to two groups of equal number. Each group comprised five experimentally naïve subjects.

Apparatus The rectangular pool was identical to the one used for Experiment 1. The landmark was a black plastic rod and identical to that used by Pearce et al (2001). The rod was 1 cm in diameter. It was attached directly to the platform and positioned on its centre. The rod stood 14 cm above the surface of the platform. Attached to the top of the rod was a white horizontal circular disc that was 4 cm in diameter and 0.5 cm thick. A second landmark was constructed which was attached to a metal base and its appearance above the surface of the water was identical to the landmark attached to the platform.

Procedure During the first 10 sessions of training the groups were required to escape from the pool by swimming to a single platform with a landmark attached to it that was situated in either one of two geometrically equivalent corners of the pool. The method used for the positioning the platform matched that used for Experiment 1. For half the subjects in each group the platform was located in the corner with the short wall to the left of the long wall. For the remaining subjects the other corner was used. A second landmark was located in the pool for Group Two Landmarks. It was in an equivalent position to the first landmark, but in the corner at the end of the long wall that was adjacent to the corner containing the platform. For each session of training the rectangle was oriented twice along the North-South axis and twice along the East-West axis of the pool and was moved between these positions in random sequence.

The first three trials of session 10 were conducted in the same manner as all other training trials. The final trial of this session was a test trial, conducted in a rectangular pool but without the platform or landmark. For the test, the rectangle was oriented along the North-South axis. For the duration of this 60-s test trial the curtain remained closed. For the purposes of the test the rectangular pool was divided into four quadrants of equal size and the time spent in the correct quadrants of the pool was recorded. The correct quadrants were the quadrant of the pool previously occupied by the platform and the corner diametrically opposite to it. All other procedural details that have been omitted for the test trial were identical to those of the equivalent test conducted in Experiment 1.

Subsequent to the test, the groups were given four trials in each of the two final sessions of training. During this stage of the experiment the landmarks were removed from the pool and training took place with two platforms. The platforms occupied geometrically equivalent corners of the pool. However, the geometric properties of the corners occupied by the platforms for this stage were the reverse of that used for Stage 1. All other procedural details that have been omitted were identical to Experiment 1.

Results and Discussion

The type 1-errorr rate of p<0.05, adopted for this Chapter was the same as that used for the previous one. The groups mean escape latencies for acquisition trials from the first 10 sessions of the first experiment can be seen in figure 4.02.

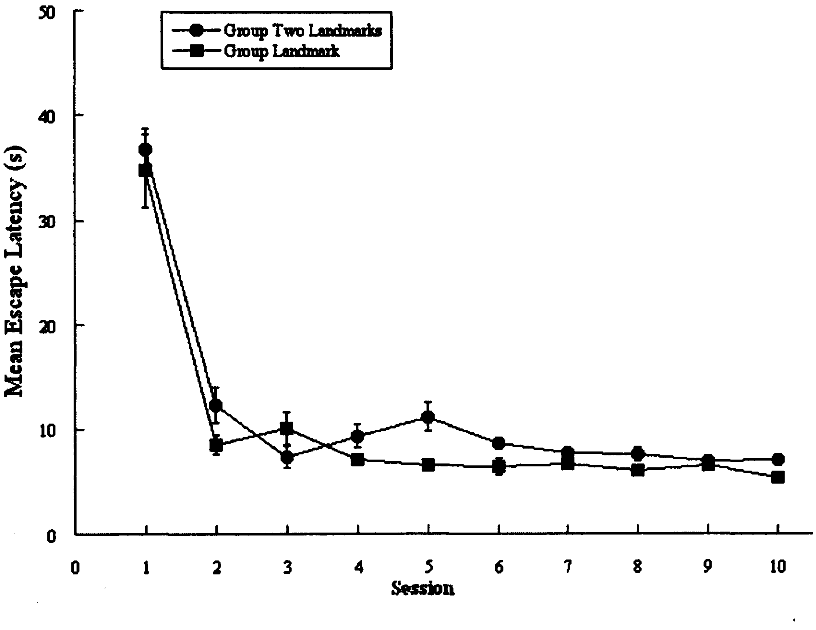

Figure 4.02. Mean escape latencies for the groups during training in the rectangular pool during Stage 1 of Experiment 7 (error bars indicate ±1 standard error of the mean).

The figure shows that escape latencies for both groups declined as sessions progressed. During every session, except the third, Group Landmark was quicker to escape onto the platform than Group Two Landmarks. A mixed two-way ANOVA of escape latencies over the 10 sessions for the two groups revealed a significant main effect of group, F(1, 18)=4.71, Mse= 29.21, p= 0.04, η_p^2= 0.21, and of session, F(9, 162)= 117.83, Mse= 13.36, p= 0.00, η_p^2= 0.87, but the interaction of Group x Session was not significant F(9, 162)=1.40, Mse= 13.36, p= 0.21, η_p^2= 0.07. One reason why Group Landmark was quicker to escape from the pool than the other group is that on every occasion they swam toward the landmark they were able find the platform. For Group Two Landmarks escape from the pool was only possible if they approached the landmark in the correct corner.

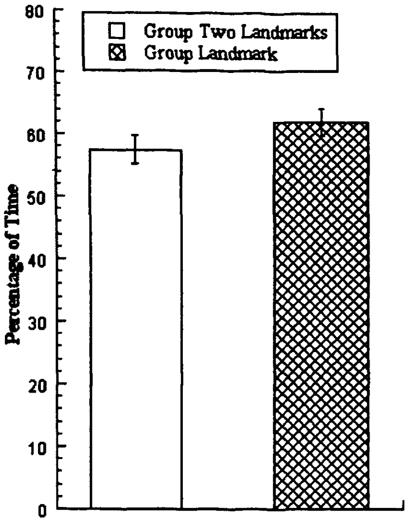

Figure 4.03. Mean percentages of time that the groups spent searching in the correct quadrants during the test in the rectangular pool without the platform and landmark/s (error bars indicate ±1 standard error).

The mean percentages of time spent in the correct quadrants of the pool during the 60 s test trial are shown in figure 4.03. One sample t-tests revealed that Group Landmark, t(9)=5.43, p=0.00, spent significantly more than 50% of the test trial searching in the correct quadrants of the pool, as did Group Two Landmarks, t(9)=3.01, p=0.00. In addition it is apparent that Group Landmark spent more time than Group Two Landmarks searching in the correct quadrants. However, a one-way ANOVA of time spent in the correct quadrants showed that this difference between the groups was not significant, F(1, 18)=1.7, Mse= 55.23, p= 0.20, η_p^2= 0.09.

Figure 4.04 shows the mean group escape latencies during the 8 trials of reversal training. From the outset and throughout this stage of the experiment Group Landmark was slower to escape onto the platform than the other group, except during the fourth trial on which the reverse outcome was found. A mixed two-way ANOVA of escape latencies over the 8 trials for the two groups showed significant main effects of group, F(1, 18) =71.45, Mse= 45.78, p= 0.00, η_p^2= 0.80, and of trial, F(2, 36)= 6.37, Mse= 55.67, p= 0.00, η_p^2= 0.26, but the interaction of Group x Trial was not significant, F(2, 36)= 2.32, Mse= 55.68, p= 0.11, η_p^2= 0.11. These results confirm that Group Landmark was slower to escape onto the platform than the other group over the final eight trials of the experiment.

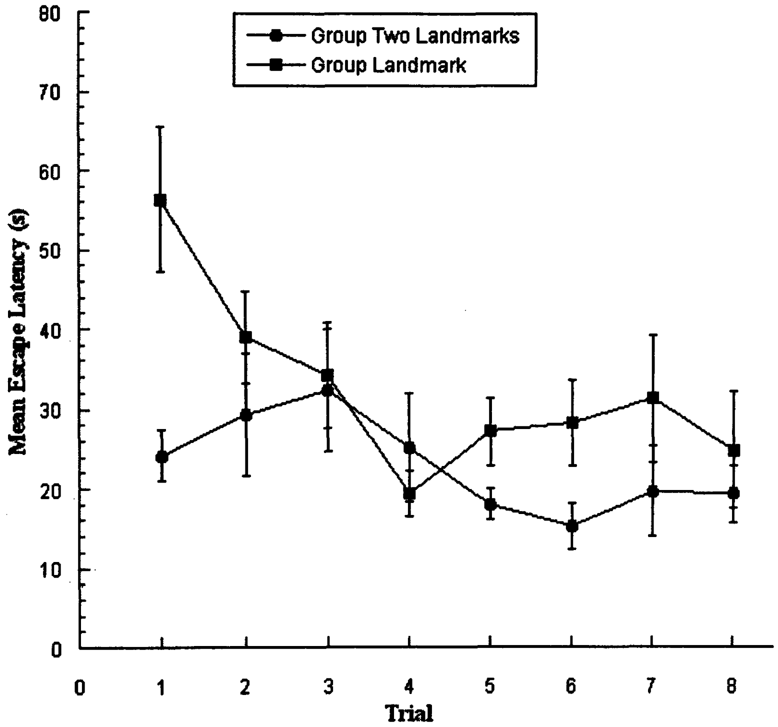

Figure 4.04. Mean escape latencies for the groups during reversal training conducted with the rectangular pool during Stage 2 of Experiment 7 (error bars indicate ±1 standard error of the mean).

One interpretation of the results from the first test is that the presence of the landmark did not detract from learning to locate the platform with reference to the shape of the pool. In fact, Group Landmark spent numerically more time searching in the correct quadrants of the pool during the test than the control group, which suggests that the landmark may have potentiated rather than overshadowed learning based on the shape of the pool.

Further evidence in support of this potentiation effect is provided by the results of the reversal training during the final 8 trials of the experiment. The results revealed that Group Landmark was significantly slower to find platform than the group trained with two landmarks, which suggests the former learned more about the original location of the platform than the latter. Not only are the foregoing results consistent with previous findings of potentiation (Durlach & Rescorla, 1980; Pearce et al, 2001; Graham et al, 2006; Hayward et al, 2003) they lend support to the view that the presence of the landmark potentiated rather than overshadowed learning based on the rectangular pool.

One way in which to explain this potentiation effect is to refer to between-stimulus associations (Durlach & Rescorla, 1981). It is possible, for example, that for the experimental group the landmark became simultaneously associated with the platform and correct corner as training progressed. Swimming toward the correct corner in the test trial would then evoke the memory of the landmark as well as the platform: encouraging rats to remain in the vicinity of the correct corner. Similar associations would have inevitably developed in Group Two Landmarks. However, for them a landmark identical to the one in the correct corner, occupied the incorrect corner of the pool and swimming towards it may have evoked the memory of the platform. This indirect association between the incorrect corner and the platform would thus serve to weaken any preference that Group Two Landmarks had for the correct corner. This difference between the groups in the preference they had for the correct corner thus explains why Group Landmark were slower than the control group to learn about the new position of the platform during the reversal training.

4.02. Experiment 8

The results of the last experiment were interpreted as providing evidence to suggest that learning based on the rectangular pool was potentiated by the presence of the landmark above the platform in Group Landmark. The primary purpose of the foregoing experiment was to test if the potentiation observed in Experiment 7 resulted from the development of between-stimulus associations (Durlach & Rescorla, 1981). To this end the design of Experiment 8 was based on that conducted by Speers et al (1980), mentioned earlier. Two groups of rats were trained first to find a submerged platform, with a landmark attached to it, located in one corner at the base of a triangular-shaped pool (see figure 4.05, left-hand panel). There were primarily two reasons for using a triangular-shaped rather than a rectangular pool. First it would ensure that the correct corner and the landmark became equally effective as cues for finding the platform. Second, it would limit any generalisation occurring between the two stages of the experiment.

Subsequent to training with the triangular-shaped pool the groups were required to escape onto a submerged platform located toward one end of a narrow rectangular arena (see figure 4.05, central column). For Group Unchanged, the platform remained beneath the landmark. The landmark thus remained an effective cue for finding the platform during Stage 2. As a result its conditioned properties were likely to remain unchanged from Stage 1 training. For Group Re-evaluate the landmark was located at the opposite end of the pool to that occupied by the platform which was intended to reduce the effectiveness of the landmark as a cue for finding the platform. In fact, it was hoped that by the end of Stage 2 Group Re-evaluate would relinquish any tendency they had for approaching the landmark.

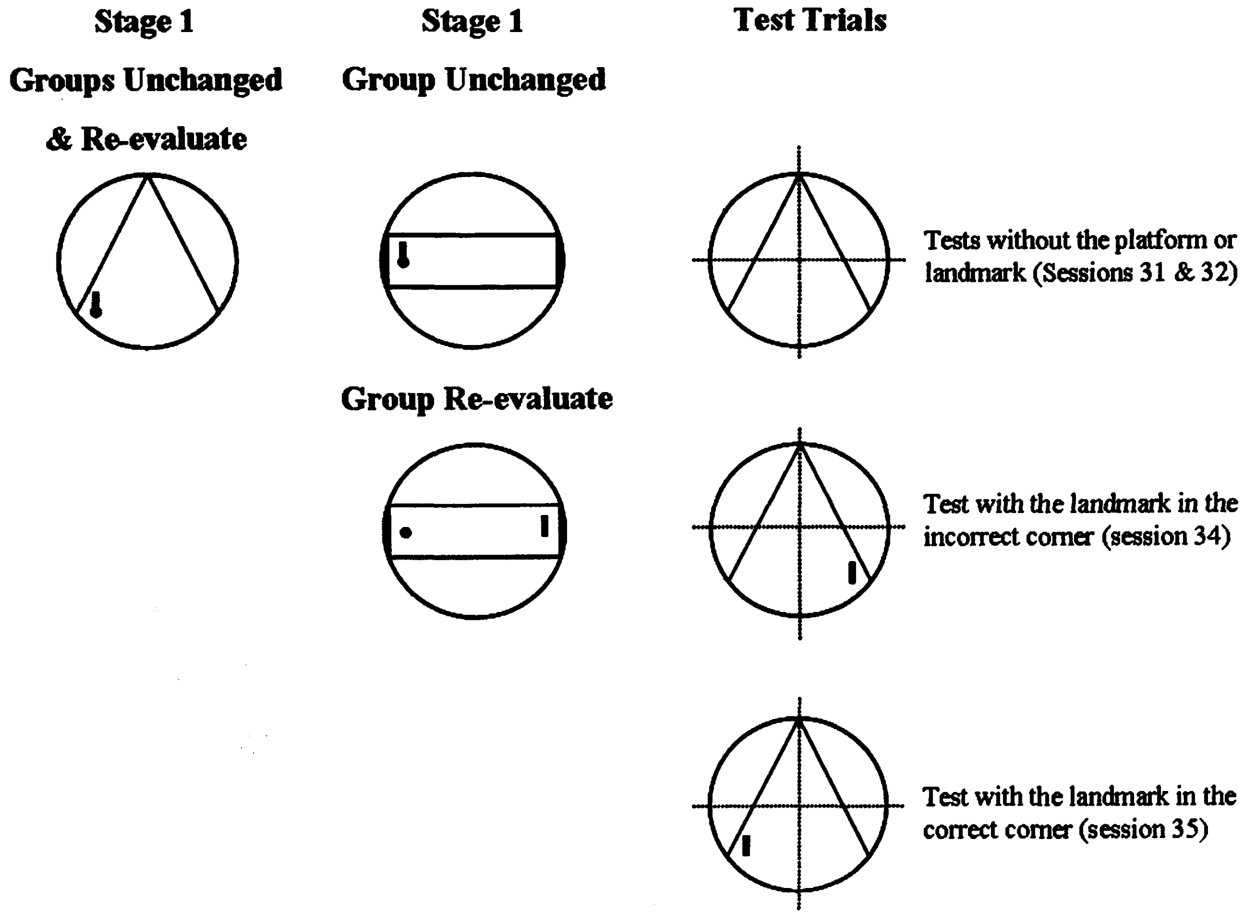

Figure 4.05. The design and apparatus used for Experiment 8. The location of the platform is given by the filled black circle. The short vertical lines indicate the position of the landmark.

Following training with the rectangular arena the groups were given a test trial conducted in the triangular-shaped pool without the landmark or platform (see figure 4.05, right-hand column). For the test the percentage of time subjects searched the correct corner: that previously occupied by the platform, was recorded. If an association had developed between the shape of the pool and landmark during Stage 1, and it was sufficiently strong to influence performance in the test; then there are empirical (Durlach and Rescorla, 1980; Pearce et al, 2001) and theoretical (Rescorla, 1980) reasons to believe that Group Unchanged should exhibit a stronger preference for swimming in the correct corner of the triangular-shaped pool than the other group. It is possible, for example, that training in Stage 1 may have resulted in the landmark becoming associated with the correct corner whilst also simultaneously becoming associated with the platform. Such associations would form in both groups and swimming in the correct corner during the test trial would evoke the memories for the platform and landmark. These memories would encourage Group Unchanged to persist searching the correct corner during the test, because for them the landmark could be used to find the platform in both stages of the experiment. The conditioned properties of the landmark were, however, modified in Stage 2 for Group Re-evaluate. Activating the memory of the landmark during the test would thus discourage these rats from persistently searching for the platform in the correct corner.

The experiment concluded with two further tests, conducted in the triangular-shaped pool with the landmark present (see figure 4.05, right-hand column). For the second test, the landmark was placed in the corner it had occupied during Stage 1 and in the third the other corner at the base of the triangular-shaped pool contained the landmark. The purpose of these tests was to assess the efficacy of Stage 2 training. If

Stage 2 training had been successful in reducing the effectiveness of the landmark as a cue for finding the platform, Group Re-evaluate might be expected to spend considerably less time than the other group searching in the quadrant of the pool containing the landmark. If however, Stage 2 training failed to decrease the extent to which Group Re-evaluate relied on the landmark for finding the platform then the performance of the groups during the final two tests should not differ.

Method

Subjects and Apparatus The 18 rats were of the same stock, with similar experience, of approximately the same age, and housed in the same conditions as those of the previous experiment. At the start of the experiment the rats were assigned randomly to the two groups. The triangular-shaped pool was identical to the one used for Experiment 2. During Stage 2 the two long boards of 1.8 m and the two short boards of 0.9 m that were used to construct the rectangular arena of the previous experiment were used to construct a rectangular pool that was 1.8 m long and 40 m wide.

Procedure During the first 20 sessions of training the groups were trained to find a single submerged platform located in one corner at the base of the triangular-shape pool. Attached to the platform was the same landmark used for Experiment 7. Rats were released into the pool, the triangle was rotated and the platform was positioned using the same method as that used for the second stage of Experiment 2. The left-hand corner at the triangle's base contained the platform for half the rats whilst the opposite corner was used for the remaining subjects. The curtain remained drawn around the pool throughout the experiment and all other procedural details that have been omitted were identical to Experiment 2.

For the 15 sessions of the second stage of the experiment, the groups were required to escape onto a submerged platform that was always situated near one of the rectangle's short walls. It was located twice in each end of the pool for each session and the sequence with which the platform was moved between these positions varied randomly from session to session. The centre of the platform was equidistant from the two long walls and positioned 30 cm away from the edge of the short wall on an imaginary line that bisected the rectangle's length. For Group Unchanged the landmark remained attached to the platform and was thus moved with the platform between each end of the pool. For Group Re-evaluate the landmark occupied equivalent positions at each end of the pool as the platform. These two objects were, however, always placed at opposite ends of the pool. The rectangle was positioned so the imaginary line bisecting its length was always oriented along the North-South or East-West axis of the pool. It was moved between these two positions, in a random sequence, for each trial. With the exception that rats were released into the pool from the two centre points of each long wall of the rectangle, all other procedural details were identical to the training trials of the previous experiment.

During acquisition trials with the triangular-shaped pool a record was taken of which corner a rat entered first after being released. The method used to assess when a rat entered a corner of the pool was identical to that used for Experiment 2. The correct corner, at the triangle's base, contained the platform, the incorrect corner was opposite to the one just described and the final corner was the apex. A record was also taken of which end of the pool a rat first entered after being released into the rectangular pool. For the purposes of this measurement the rectangular arena was divided, along its length, into four quadrants of equal area measuring 40 cm x 45 cm. A subject was regarded as searching in the correct quadrant of the pool when it entered the one in which the platform was located. The incorrect quadrant was the one farthest away from the one with the platform.

In Sessions 31 and 32 the first three trials were conducted in the same manner as all other training trials that took place in the rectangular pool. The fourth trial of these sessions took place in the triangular-shaped pool without the landmark or the platform. The triangle was oriented so that its apex pointed South in relation to the experimental room. For the tests, rats were released from the centre of the pool and were permitted to swim freely for 60 s. To assess the performance of rats during the tests, the triangle was divided into four quadrants of unequal size and the time that rats spent in each quadrant was recorded (see figure 4.05, right-hand panel). The correct corner was always the one at the base of the triangle that previously contained the platform, whilst the other corner at its base was the incorrect one.

During Session 33 and for the first three trials of the final two sessions, the groups received training with the rectangular pool identical to that given on previous occasions. Two further tests were conducted on the fourth trials of sessions 34 and 35. For these tests the landmark without the platform was placed in one corner at the base of the triangular-shaped pool. In the first test the landmark occupied the corner that contained the platform during Stage 1, whilst in the second it occupied the other corner at the base of the triangular-shaped pool. Despite this difference between the tests, they were carried out in an identical manner to the previous tests conducted with the triangular-shaped pool.

Results and Discussion

The group's mean escape latencies for acquisition trials that took place in the triangular-shaped pool during the first 20 sessions of the experiment can be seen in figure 4.06 (left-hand side). Both groups showed a marked decrease in their escape latencies over these sessions of training. A mixed two-way ANOVA of escape latencies over the 20 sessions for the groups showed a significant main effect of session, $\underline{F}(19, 304)=105.78$, Mse= 16.63, $\underline{p}= 0.00$, $\eta_p^2= 0.87$, a significant interaction of Group x Session, $\underline{F}(19, 304)=3.36$, Mse= 16.63, $\underline{p}=0.00$, $\eta_p^2= 0.17$, but the main effect of group was not significant, $\underline{F}(1, 16)= 0.22$, Mse= 12.93, $\underline{p}=0.64$, $\eta_p^2=0.01$. Simple effects tests showed that there were significant differences between the groups at sessions 1, $\underline{F}(1, 320)= 55.36$, Mse= 16.44, $\underline{p}= 0.00$, $\eta_p^2= 0.15$, and 3, $\underline{F}(1, 320)= 4.88$, Mse= 16.44, $p= 0.03$, $\eta_p^2= 0.02$, but during all other sessions their performance was indistinguishable $\underline{Fs}<1$. The difference between the groups during sessions 1 and 3 was unexpected and difficult to explain. However, the similar performance of the groups during the remainder of Stage 1 suggests that their initial differences were unlikely to influence the outcome of the experiment.

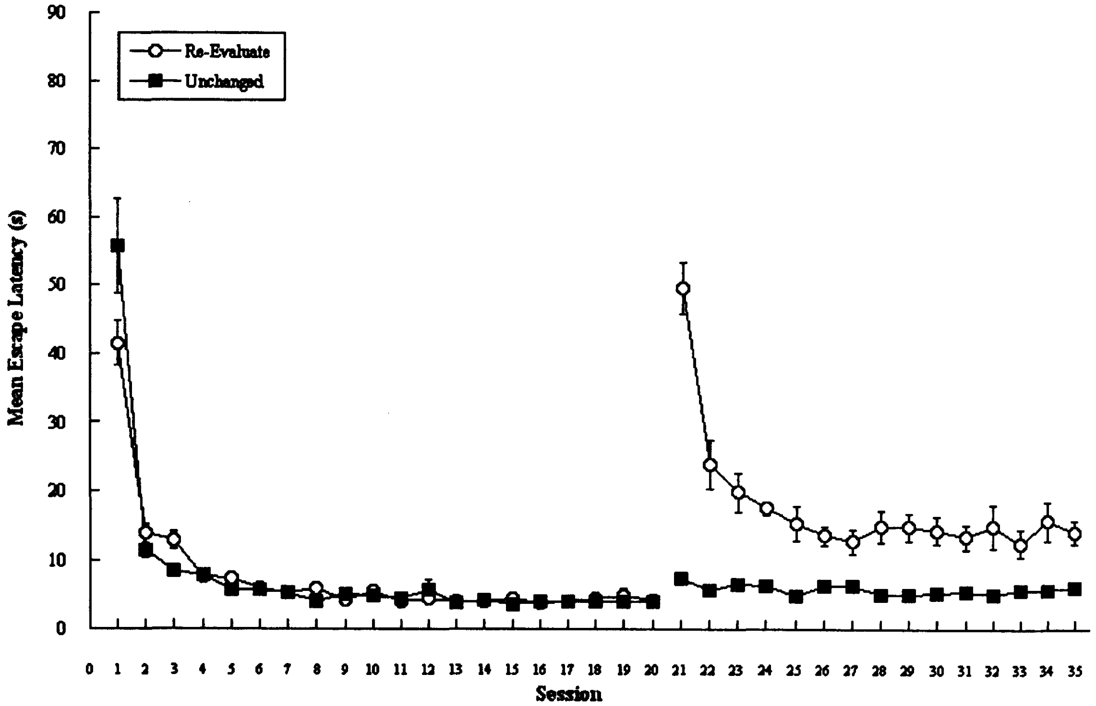

Figure 4.06. Mean escape latencies for the groups during training with the triangular-shaped pool during Stage 1(left-hand side) and with rectangular pool during Stage 2 pool (right-hand side) of Experiment 8 (error bars indicate ±1 standard error of the mean).

Figure 4.06 (right-hand side) shows the group's mean escape latencies for acquisition trials that took place in the rectangular arena during the final 15 sessions of the experiment. During every session Group Unchanged found the platform more quickly than Group Re-evaluate. Training rats with the landmark attached to the platform in Stage 1 enabled Group Unchanged to identify the corner containing the platform from the outset of the second stage. By comparison the ability of Group Re-evaluate to find the platform at the outset of Stage 2 was impaired. A mixed two-way ANOVA of escape latencies over the 15 sessions of training for the two groups, revealed that Group Unchanged was significantly quicker to escape from the pool onto the platform than Group Re-evaluate, $F(1, 16)=47.80$, Mse= 208.67, $p= 0.00$, $\eta_p^2= 0.75$. The ANOVA also showed a main effect of session, $F(14, 224)= 29.51$, Mse= 14.61, $p= 0.00$, $\eta_p^2= 0.65$, and significant interaction of Group x Session, $F(14, 224)=24.86$, Mse= 14.61, $p= 0.00$, $\eta_p^2= 0.61$. Simple effects tests showed that the effect of session was significant for Group Re-evaluate, F(14, 224)=54.06, Mse= 14.61, p= 0.00, η_p^2= 0.77, but not for Group Unchanged, F(14, 224)= 0.31, Mse= 14.61, p= 0.99, η_p^2= 0.02. These latter findings confirm that the performance of Group Re-evaluate improved as training progressed but remained relatively constant for Group Unchanged. Additional tests of simple effects revealed that on every session Group Unchanged found the platform more quickly than Group Re-Evaluate Fs (1, 240)$\geq$6.78.

The above results imply that both groups had learned to use the landmark to find the platform by the end of Stage 1. Approaching the landmark at the beginning of Stage 2 enabled Group Unchanged to escape from the pool because for them the landmark continued to be attached to the platform. For Group Re-evaluate, however, the landmark and platform always occupied opposite ends of the pool during the second stage. Approaching the landmark thus interfered with escaping from the pool. Even so, Group Re-evaluate must have relinquished their tendency to approach the landmark because their escape latencies were significantly quicker by the end of Stage 2, which implies the conditioned properties of the landmark were successfully modified.

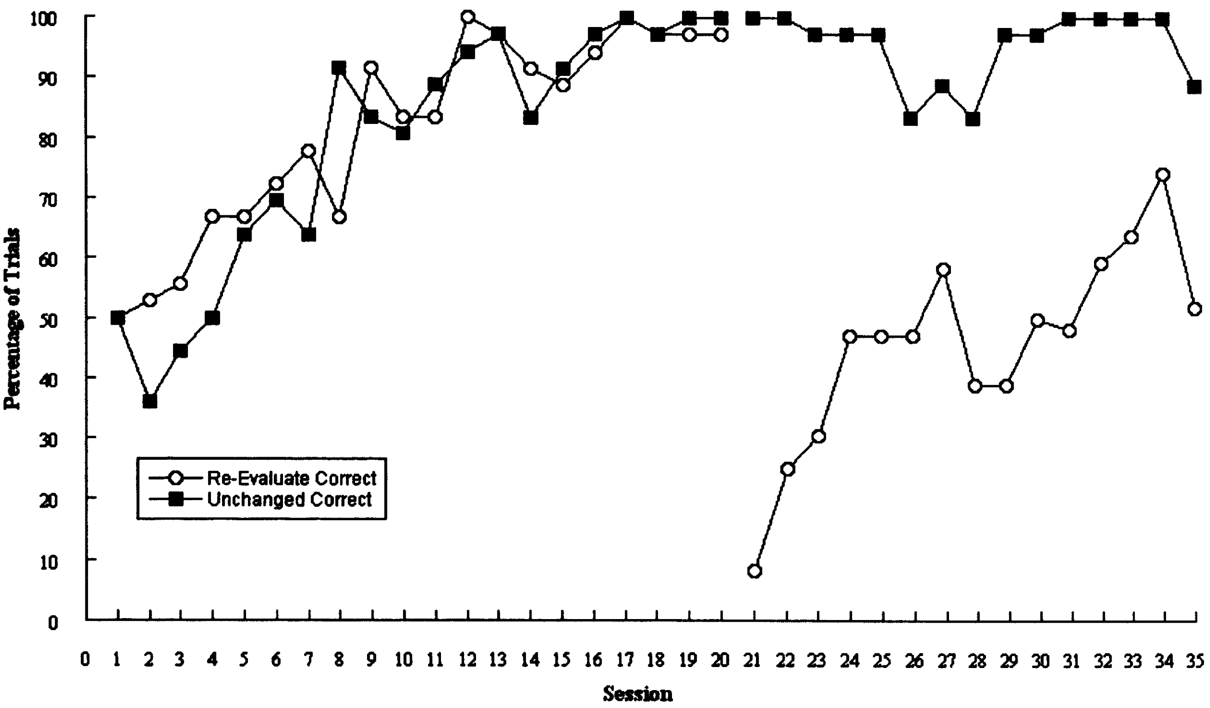

Figure 4.07 Mean percentages of trials the groups entered first the corner of the triangular-shaped pool containing the platform during Stage 1 (left-hand side) and the end of the rectangular pool containing the platform during Stage 2 (right-hand side) during Experiment 8.

Figure 4.07 (left-hand side) illustrates the mean percentages of trials the groups entered first the correct corner of the triangular-shaped pool. Both groups learned quickly to find the platform and by the end of Stage 1 differences between the groups were negligible. To compare the performance of the groups the mean percentages of trials on which individual subjects swam directly to each of the three corners of the triangular-shaped pool was calculated for the first 20 sessions combined. For the correct corner, the incorrect corner and the apex these percentages were; 81.53, 6.53 and 11.94 for Group Unchanged and; 79.17, 8.05 and 12.78 for Group Re-evaluate, respectively. Between group comparisons revealed that the groups entered the correct, incorrect and apex corners equally often (Us (9, 9) ≤19), which confirms differences between the groups were not apparent. Within group comparisons revealed that Group Re-evaluate entered first the correct corner more often than either the incorrect corner or the apex, (Ts(9)≤43), as did Group Unchanged,(Ts(9)≤44). These analyses confirm that both groups discriminated the corner containing the platform from the other corners of the pool. Both groups swam first to the opposite and apex corners equally often (Ts(9)=6).

The right-hand side of Figure 4.07 shows the mean percentages of trials on which rats swam first directly to the quadrant occupied by the platform after being released into the rectangular pool during Stage 2. It is apparent that training with the landmark attached to the platform in Stage 1 enabled Group Unchanged, but not Group Re-evaluate to identify the corner containing the platform from the outset and throughout the second stage. The performance of Group Re-evaluate improved as sessions progressed which implies that rats gave up the strategy they had for heading toward the landmark to find the platform.

To compare the performance of the groups, the mean percentages of trials on which individual subjects swam directly to the correct and incorrect quadrants of the rectangular pool was calculated for the 15 sessions combined. For the correct and incorrect quadrants these percentages were: 95.4 and 4.6 for Group Unchanged; and 45.9 and 54.1 for Group Re-evaluate respectively. Between Group comparisons revealed that Group Unchanged swam first to the correct quadrant of the pool significantly more often than Group Re-evaluate U (9,9)=4. The incorrect quadrant was entered first significantly more often by Group Re-evaluate than by Group Unchanged U (9,9)=0. Together these analyses suggest that the landmark retained its control over searching for the platform in Group Unchanged, but it was weakened by the training given to Group Re-evaluate during Stage 2.

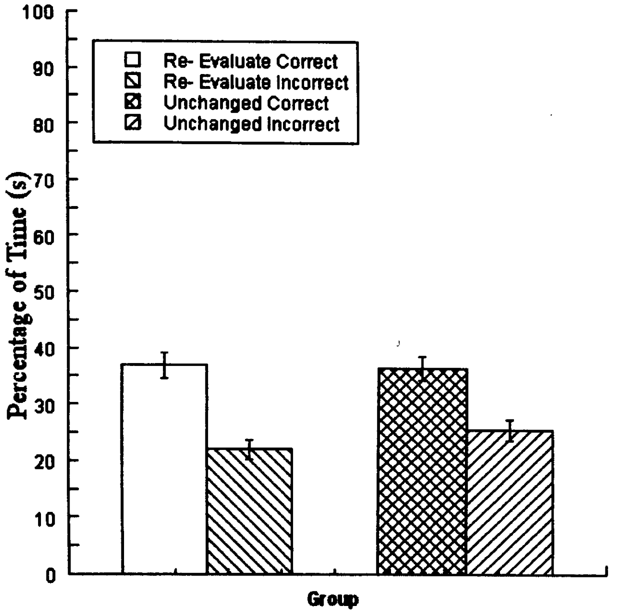

Figure 4.08. Mean percentages of time the groups spent searching in the correct and incorrect quadrants of the triangular-shaped pool during the test without the platform or landmark (error bars indicate ±1 standard error).

Three test tests were given to rats over the course of the experiment. Rats were tested first in the triangular-shaped pool without the landmark and platform. Two such tests, during sessions 31 and 32, were carried out. The mean percentages of time rats spent searching in the correct and incorrect quadrants of the pool for the tests combined are illustrated in figure 4.08. For the purpose of the test the correct quadrant was the one that contained the platform during Stage 1. The incorrect quadrant contained the other corner at base of the triangle. The groups showed a preference for searching the correct quadrant of the pool and differences between the groups were not apparent. A two-way ANOVA for the groups, and of time spent in the correct and incorrect quadrants showed a main effect of quadrant, $F(1, 16)=29.13$, Mse= 50.89, $p= 0.00$, $\eta_p^2= 0.65$, but neither the main effect of group, $F(1, 16)= 0.96$, Mse= 21.1, $p= 0.34$, $\eta_p^2= 0.06$, nor the interaction of Group x Quadrant $F(1, 16)= 0.72$, Mse= 50.89, $p=0.41 \eta_p^2= 0.04$, was significant.

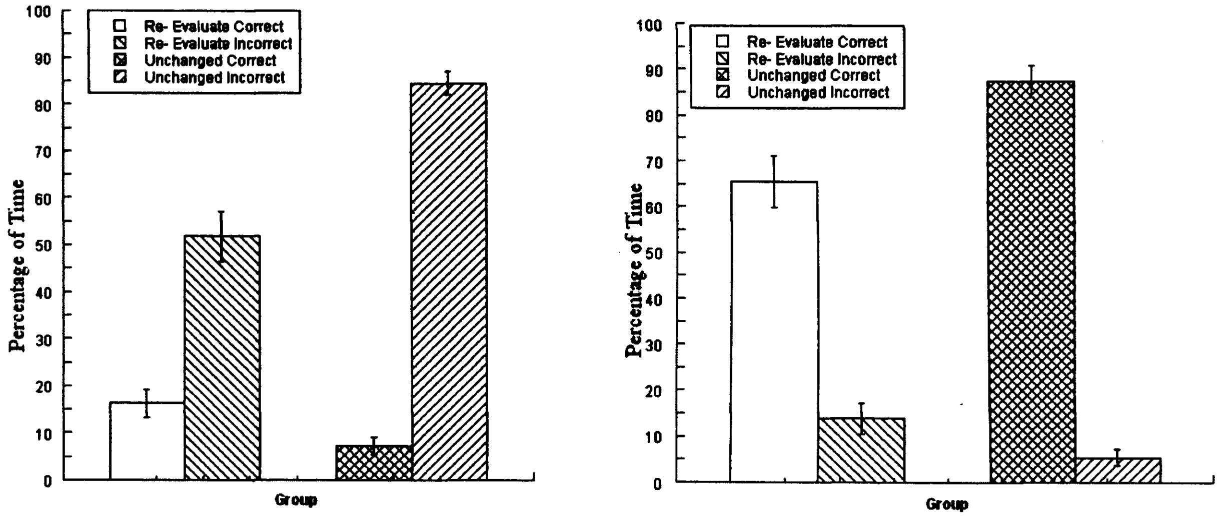

Figure 4.09. Mean percentages of time the groups spent searching the correct and incorrect quadrants of the triangular-shaped pool during the tests when the landmark occupied the incorrect (left-hand panel) and correct quadrants (right-hand panel) of the pool. Each test was conducted without the platform (error bars represent ±1 standard error of the mean).

At first sight the results imply that training Group Re-evaluate without the platform beneath the landmark in Stage 2, failed to influence spatial learning based on the triangular-shaped pool. However, there may be other reasons why the groups behaved in a similar manner during the tests and these shall be discussed later.

Figure 4.09 (left-hand panel) shows similar data for the test conducted on the final trial of session 34. For this test the correct quadrant was again the one which had contained the platform during the first stage. The landmark occupied the other quadrant at the base of the triangle and this quadrant was considered to be the incorrect one. It is apparent that the groups spent more time searching the incorrect than the correct quadrant of the pool. However, Group Re-evaluate spent considerably less time than Group Unchanged searching in the quadrant that contained the landmark. This outcome suggests that the training designed to decrease the extent to which Group Re-evaluate relied on the landmark as a cue for finding the platform was successful. A two-way ANOVA of the time spent in the correct and incorrect quadrants of the pool showed significant main effects of group, F(1, 16)=31.67, Mse= 39.97, p= 0.00, η_p^2= 0.66, of quadrant, F(1, 16)=170.91, Mse= 167.80, p= 0.00, η_p^2= 0.91, and a significant interaction of Group x Quadrant, F(1, 16)=23.57, Mse=167.80, p= 0.00, η_p^2= 0.60. Simple effects tests revealed that Group Re-evaluate spent significantly more time in the correct rather than incorrect quadrant of the pool, F(1,16)=33.78, Mse= 167.80, p= 0.00, η_p^2= 0.68, as did Group Unchanged, F(1, 16)=160.70, Mse= 167.80, p=0.00, η_p^2= 0.91. Finally, Group Re-evaluate spent significantly less time than the other group searching in the quadrant of the pool containing the landmark, F(1,32)= 46.70, Mse= 103.89, p= 0.00, η_p^2= 0.59. Taken together these results suggest that relative to Group Unchanged, Group Re-evaluate tended to avoid searching in the corner of the pool with the landmark. It thus appears that Stage 2 training successfully reduced landmark control in Group Re-evaluate.

The equivalent data for the test undertaken on the final trial of session 35 are presented in the right–hand panel of figure 4.09. For this test the correct quadrant was once again the one occupied by the platform during Stage 1, but on this occasion it contained the landmark. Like the previous test rats spent more time searching in the quadrant of the pool with the landmark than the other corner at the base of the triangle. In addition Group Re-evaluate spent less time than Group Unchanged searching in the quadrant of the pool with the landmark. This observation once again points to the success of the training given to Group Re-evaluate during Stage 2. A two-way ANOVA of time spent in the correct and incorrect quadrants by the groups, showed significant main effects of group, F(1, 16)=8.77, Mse= 47.43, p= 0.00, η_p^2= 0.35 and of quadrant, F(1, 16)=187.40, Mse= 214.02, p=0.00, η_p^2= 0.92, as well a significant interaction of Group x Quadrant, F(1, 16)=9.70, Mse= 214.02, p= 0.00,

η_p^2= 0.38. Simple effects tests revealed that Group Re-evaluate, F(1, 16)=55.91, Mse= 214.02, p= 0.00, η_p^2=.78, and Group Unchanged, F(1, 16)=141.20, Mse= 214.02, p=0.00, η_p^2= 0.90, spent significantly more time searching in the quadrant that contained the landmark than the incorrect quadrant of the pool. Importantly Group Re-evaluate spent significantly less time searching in the quadrant of the pool with the landmark than the other group, F(1, 32)=16.64, Mse= 130.73, p=0.00, η_p^2= 0.34. The latter finding confirms that relative to Group Unchanged, Group Re-evaluate avoided swimming in the quadrant of the pool with the landmark.

Despite the presence of the landmark above the platform during the first stage of the experiment, there is clear evidence to suggest that the shape of the pool was used by rats to identify the location of the platform. Not only did rats swim first more often to the correct corner during training, they also showed a preference for this corner during the tests in the triangular-shaped pool without the landmark or platform. Together these results imply that the landmark failed to detract from learning based on the shape of the pool. This conclusion is consistent with the previous failures to find cue competition between featural and geometric cues (for example, Cheng, 1986; Kelly et al, 1998; Pearce et al, 2001).

The results provided by Stage 2 imply that Group Re-evaluate reduced their tendency to approach the landmark even though they had used this cue to find the platform in Stage 1. The training intended to reduce the effectiveness of the landmark as a cue for finding the platform, thus proved to be successful. The question is then raised why did Stage 2 training fail to influence spatial learning based on the triangle?

One answer to the above question is that associations may have failed to develop between the landmark and the shape of the pool during Stage 1. If this was the case then swimming toward the correct corner of the triangle during the test would be expected to activate only the memory for the platform. The memory for the landmark and its conditioned properties would remain inactive. As a result there would be no means by which Stage 2 training could influence the behaviour of either group during the test and any preference rats had for the correct corner would be similar. Even so, there may several other ways in which the test results might be explained and these are discussed in the general discussion below.

4.03. General Discussion

Experiment 7 revealed that the landmark attached to the platform did not detract from spatial learning based on the rectangular pool. Instead the experiment provides evidence to suggest that learning based on the rectangle was, to some extent, potentiated by the landmark. This evidence is provided first by the results of the test trial conducted in the rectangular pool in the absence of the landmark and platform. In that test Group Landmark spent numerically more time searching in the correct quadrants of the pool than the control group, but this result was not statistically significant.

Further evidence for the potentiating effect of the landmark was supplied by the results of the final eight trials of training, during which two platforms occupied corners of the pool that differed, geometrically, to the one that contained the platform during Stage 1. This reversal was acquired more slowly by Group Landmark than the control group, which suggests the former learned more about the original location of the platform than the latter. These results are consistent with those supplied by Pearce et al (2001) and extend them by showing a landmark can also potentiate learning based on a rectangular pool.

The primary purpose of Experiment 8 was to assess whether the potentiating effect of the landmark observed in Experiment 7 could be explained by appealing to the development of between-stimulus associations. Experiment 8 provided sufficient evidence to suggest that the training given to Group Re-evaluate during Stage 2 successfully reduced the effectiveness of the landmark as a cue for finding the platform. Even so, there were no observable differences between the groups when they were tested in the triangular pool without the platform or landmark. One interpretation of this result is that an association failed to develop between the landmark and triangular-shaped pool in Stage 1, making any further training with the landmark irrelevant. Consequently it is implausible that any potentiation found in Experiment 7 resulted from the occurrence of between-stimulus associations.

There are, however, several other ways in which the absence of between group differences observed in the first two tests of Experiment 8 might be explained. One possibility is that the tests were not sufficiently sensitive to detect the influence of Stage 2 training. This explanation deserves little merit, however, because the final two tests, being conducted in a similar manner to the first two, did reveal differences between the groups. Another possibility is that a generalisation decrement resulting from the removal of the landmark may have disrupted spatial learning based on the shape of the pool during the first, but not final tests. The disruptive effect of landmark removal might have therefore contributed to the failure to reveal the influence of between-stimulus associations in the first tests.

Although the tendency of Group Re-evaluate to approach the landmark had markedly been reduced by the end of Stage 2, this group still showed a preference for the corner containing the landmark in the final two tests, albeit to a lesser extent than Group Unchanged. Thus, despite reducing the effectiveness of the landmark as a cue for finding the platform, it still controlled the behaviour of Group Re-evaluate. The training given in Stage 2 thus served to weaken the relationship between the landmark and the platform, but failed to abolish it completely.

Giving more training trials in the second stage may have overcome the above problem but at the risk of increasing yet another. It is possible that Stage 2 training may have weakened, in both groups, any associations which may formed between the triangle and the landmark during Stage 1. Freberg (1979) has shown that the strength of a between-stimulus association is markedly reduced when one element of a compound stimulus is presented on its own. Presenting the landmark on its own in Stage 2, may thus have weakened the relationship between the landmark and the triangular-shaped pool. Any weakening of this between-stimulus association would occur equally in both groups and influence the behaviour of rats during the test trials. In support of this proposal it is worth noting that subjects received many trials with the landmark in Stage 2. Moreover, the preference rats exhibited for the correct corner during the test in the triangular pool without the landmark and platform was relatively small. Decreasing the number of the trials given in Stage 2 would have limited the possibility of compromising the landmark-triangle association, but at the risk of leaving the conditioned properties of landmark in Group Re-evaluate unchanged. Just how many trials are needed to re-value the conditioned properties of the landmark whilst also leaving landmark-triangle association intact is uncertain and perhaps needs to be explored in future experiments.

One shortcoming of the final experiment is that it is difficult to assess whether spatial learning based on the triangular-shaped pool was influenced by the presence of the landmark. In hindsight it would have been prudent to include a control group which was trained first to find the platform in one corner of the triangular-shaped pool but without the landmark attached to it. For Stage 2 training in the rectangular pool the landmark could have remained above the platform. Alternatively the platform and landmark could have occupied opposite ends of the pool. Importantly, neither of these methods for training rats in Stage 2 would be expected to influence spatial learning based on the triangle because the landmark was absent during first stage. As a result this new control group would have provided a suitable yard stick to assess whether the degree of learning based on the triangle had been influenced by the presence of the landmark in the other two groups.

Unfortunately, the absence of a suitable control group hinders any interpretation of the results supplied by the final experiment. Even so, Groups Unchanged and Re-evaluate did exhibit a similarly strong preference for the correct corner of the triangle in the tests without the landmark. On the face of it such an outcome implies that between-stimulus associations failed to develop or if they did develop, then their influence over the behaviour of subjects was rather weak. This failure of the landmark to influence spatial learning based on the shape of an environment in general agreement with predictions taken from the Geometric Module theory (Cheng, 1986; Gallistel, 1990). It is less consistent with the Rescorla-Wagner model (1972). However, with improved experimental design associative learning might offer suitable explanations for the present results.

Part II

Chapter 5.

5.01. Is Navigation Based on Local or Global Cues?

According to predictions derived from the theory of the Geometric Module (Cheng, 1986; Gallistel, 1990) learning based on the shape of an environment should be largely unaffected by any featural cue placed within it. The repeated failures to find cue competition described in Part I are consistent with this point of view, whilst at the same time sit uncomfortably with associative learning theories such as the Rescorla-Wagner model (1972) . Another assumption underlying the theory of the Geometric Module is that animals should find their way to a hidden goal by referring to a global representation of the cues surrounding it, rather than by using them in a more restricted or local manner (Cheng, 1986; Gallistel, 1990). Thus, if it can be shown that animals navigate with reference to local cues then this would not only challenge the proposals of Cheng and Gallistel but it would also prompt an alternative explanation for the failures to find cue competition found in the previous chapters and elsewhere (Cheng; Pearce et al, 2001; Kelly et al 1998; Graham et al, 2006). Finally according to associative learning theories (Rescorla & Wagner, 1972) Pavlovian conditioning results from the formation of an association between individual CSs and the US which implies animals should use local rather than global cues to find their way around.

The overall purpose of Part II is to assess whether animals navigate with reference to the overall shape of an environment. I shall begin by describing, albeit briefly, studies showing that animals can navigate effectively with reference to a single landmark (Collett, Cartwright & Smith, 1986). If they can accomplish this they might also rely on a single landmark to navigate when it is accompanied by several others, ignoring global cues such as the shape which together they describe. Following a discussion of the latter issue I move on to consider experiments in which animals have been trained to find a goal in one shape and are then tested with a transformed version of the original (Tommasi & Vallortigara, 2000; 2001; Tommasi, Vallortigara & Zanforlin, 1997; Gray, Spetch, Kelly & Nguyen, 2004; Tommasi & Polli, 2004; Esber, et al 2005; Pearce, Good, Jones, McGregor, 2004; McGregor, Jones, Good & Pearce, 2006). I finish this section by describing one of my own experiments, the findings of which imply that animals use local rather than global cues to navigate.

5.02. Navigation with reference to a Single Landmark

Even though Cheng (1986) and Gallistel (1990) have assumed that animals navigate with reference to global cues there is much evidence to suggest they can find their way to a hidden goal by referring to the cues surrounding it in a more restricted or local manner. One good example of this behaviour is provided by Collett et al (1986) who showed that animals found a hidden goal by referring to a single landmark. They trained gerbils to find a sunflower seed that was hidden in the floor of a circular arena. The food was always located at the same distance and direction from a white cylinder that acted as a landmark and together they were moved as a unit to various places around the arena for each trial. In addition subjects were released from different positions around the arena so it was difficult for them to learn a specific route to the food. Nevertheless, by the end of training they had learned to retrieve the food, presumably by referring to the landmark. Rats can also navigate with reference to a single landmark and this behaviour has been found in a watermaze task (Pearce, Roberts and Good, 1998) and a task during which food was hidden on the floor of a square arena (Biegler & Morris, 1993; 1999).

Collett et al argued (1986) their subjects found the food by using a vector based on the cylinder, with the vector providing the distance and direction of the goal from the landmark. It must be noted that Collett et al (1986) and Pearce et al (1998) used cylindrical and spherical landmarks respectively, which by themselves could not be used to establish heading. Instead this information must have been acquired by the experimental room surrounding the apparatus. By comparison, due to its shape the irregular tetrahedron used by Biegler and Morris (1993) could be used as a cue to determine heading.

Given the above results (Collett et al, 1986; Pearce et al, 1998; Biegler & Morris, 1993), it is not unreasonable to suppose that when a hidden goal is surrounded by several landmarks animals will refer to just one of them in order to find it. Empirical evidence tends to support this point of view. Recall, for example, the study conducted by Spetch and Wilkie (1994) in which pigeons received food for pecking the hidden goal area of a touch screen, the position of which was fixed relative to three different landmarks: a log, a flower and a tree; the latter being closest to the goal. When presented with modified versions of the array for tests, pigeons search accuracy declined in response to the removal or shift of the tree and no other landmark. On the basis of these results it was argued that the tree controlled searching. It is worth pointing out that the absence or relocation of the landmarks altered the shape of the array for the tests, making it unlikely that geometric cues controlled behaviour. Hence, searching must have been based on local rather than global cues.

Another example of this use of local cues can be found in the study undertaken by Garrod-Cole et al (2001) who required an experimental group of infants to find a toy hidden in one corner of a rectangle described by four boxes of unique colour and pattern. During acquisition infants searched predominantly in the correct corner for the toy. Errors of searching at the other three corners were evenly distributed between them. There was thus no hint that searching was based on the overall shape of the apparatus. Instead the features of the box containing the toy controlled searching. These results imply that the cues surrounding the toy were used in a restricted rather than a global manner.

5.03. Shape Transformation Experiments

Other experiments to test whether animals navigate with reference to local or global cues have adopted a transformation approach. In these studies animals are trained to find a goal hidden, for example, at the centre of an environment with a distinctive shape which is then transformed in some way or other for testing. The logic to this approach is simple: if animals should persist searching at the centre of the transformed arena, then it is unlikely that the overall shape of the original apparatus was used to find the goal. Such experiments fall broadly into two categories: those in which environmental geometry is provided by an array of landmarks and those in which it is supplied by an arena with enclosed walls. For simplicity I shall discuss the former before the latter.

5.04. Shape Transformation Experiments with Landmark Arrays

One study to adopt the transformation approach was conducted by Spetch, Cheng and Macdonald (1996). They trained pigeons to peck a hidden goal area of a touch screen for food; the goal being located at the centre of square described by an array of four different 2-dimensional graphic landmarks (see figure 5.01, top row). For Group Fixed each landmark remained in the same location throughout training. They could therefore find the goal by referring to either the shape of the array or any landmark within it. For Group Rotate, the landmarks were moved between the corners of the square for each trial so that each landmark appeared equally often in every corner of the array. As a result this group was expected to refer to the overall shape of the array to find the goal. The results of non-reinforced test trials suggest, however, that Group Rotate adopted a rather different approach to find the goal.

For all the following tests the groups were presented with identical stimuli in which the four landmarks occupied the same corners of the square as they did for Group Fixed during training. In addition the array occupied a new location on the screen to prevent pigeons from using it as a cue to find the goal. In a control test the size and shape of the array remained unchanged. Under these conditions the groups, who did not differ, showed a preference for searching at the centre of the array. Some aspect of the array must have therefore controlled searching.

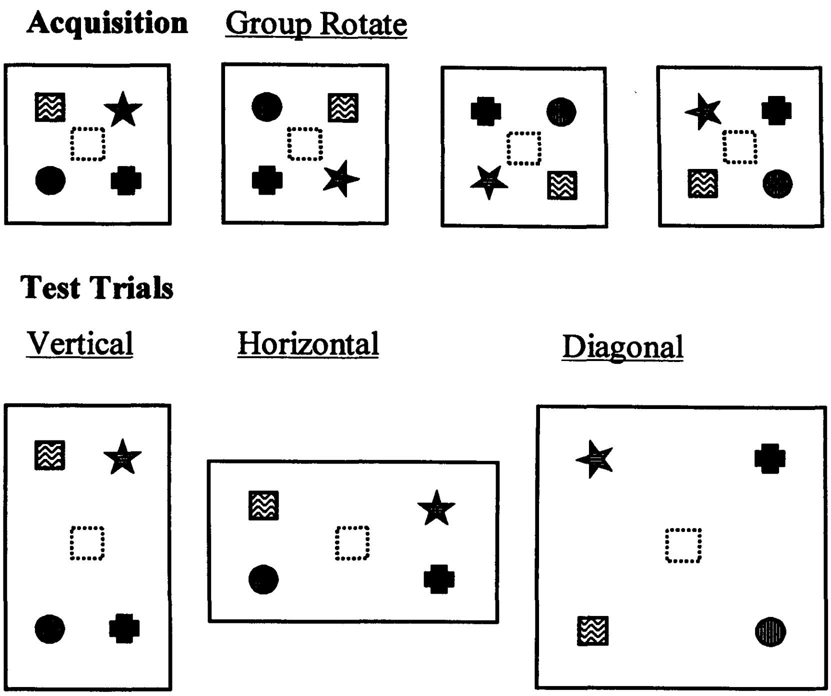

Figure 5.01. The appearance of the stimuli used by Spetch et al (1996). All stimuli were presented on touch screen. The geometric shapes denote the four different 2-dimensional landmarks. The top row shows each of the four presentations Group Rotate received during training. The dotted boxes indicate the hidden the goal areas. The bottom row shows how the stimuli were arranged for the vertical, horizontal and diagonal expansion tests.

In another series of tests the array was transformed, being expanded either vertically, horizontally or diagonally (see figure 5.01, bottom row). Once again differences between the groups were not apparent but on this occasion pigeons failed to show any preference for searching at the centre of the array. Instead they pecked in locations that corresponded to the distance and direction between the goal and one of the landmarks during acquisition. Put simply, searching was not based on the overall shape of the array but on a vector from a single landmark. It is perhaps worth mentioning that pigeons' behaviour was controlled by different landmarks. The circular landmark shown in the figure 5.01, for example, controlled searching in some but not all subjects.

Searching with reference to a vector might have been expected by Group Fixed, because for this group the relationship between the goal and each landmark always remained stable. Why Group Rotate should have adopted a similar approach is perhaps more difficult to explain, since for them the relationship between each landmark and the goal was inconsistent. To account for this apparent paradox Spetch et al (1996) have argued that pigeons *"appeared to respond so as to maintain the appropriate distance from an individual landmark, using the landmark configuration to determine which direction from that individual landmark to search"* (p.62). If there is any merit to this account then it would imply that subjects found the goal by using the cues surrounding it in a local rather than global manner- thus posing problems for the theory of the Geometric Module (Cheng, 1986; Gallistel, 1990).

In a similar study Spetch, Cheng, MacDonald, Linkenhoker, Kelly and Doerkson (1997) trained pigeons to find a goal hidden at the centre of a square described by four identical landmarks. The design and methods of that experiment were much the same as those used by Spetch et al (1996), with the exception that the landmarks were 3-dimensional and placed on the floor of an experimental room which allowed pigeons to explore the apparatus. For one test, during which the size of the array was increased, pigeons searched in locations that corresponded to a vector between the goal and one of the landmarks in the original array. Thus, the finding that pigeons navigate with reference to local cues such as vectors seems to be general and reliable.

A study using a rather different apparatus was conducted by Esber et al (2005; see Experiment 9) who trained rats to escape a pool of opaque water by swimming towards a platform located in one corner of a rectangle described by four identical landmarks. For simplicity it shall be assumed that the correct corner, the one with the platform, had the long side to the right of the short side. For the testing stage the landmarks were rearranged to form a kite: making the corners where the long and short sides met right angled. One of these corners was congruent with the correct corner of the rectangular array, the other being incongruent with it.

Esber et al (2005) reasoned that if rats used a global representation of the original apparatus to search, then transforming its shape into a kite for the second stage should make it impossible for them to discriminate between the two right-angled corners of the pool. Contrary to this prediction Esber et al (2005) found that rats showed a preference for searching the congruent rather than the incongruent corner of the kite-shaped pool. Searching for the platform in both stages must have therefore been under the control of local rather than global cues. As a means of identifying what these local cues might be, a test was conducted in which the two landmarks from the short side of the rectangular array opposite to that with the platform were removed from the pool. Under these conditions rats found the platform, despite being released from the centre of the pool, which implies they the found platform in both stages by swimming towards a corner at the right-hand end of the short side. Such results add much weight to the idea that navigation was based on local rather than global cues whilst at the same time undermine predictions derived from the Geometric Module (Cheng, 1986; Gallistel, 1990).

5.05. Shape Transformation Experiments with Enclosed Environments

In the above studies environmental geometry (Spetch et al, 1996; 1997) was supplied by an array of landmarks. Some inherent property of this apparatus may have encouraged animals to navigate with reference to local cues and it is not unreasonable to suppose global cues might control behaviour when environmental geometry is supplied by an arena with a distinctive shape. One study to test this idea, conducted by Tommasi and Vallortigara (2000; 2001) was mentioned earlier. They trained chicks to find food hidden at the centre of a square arena with enclosed walls. After reaching a suitable asymptote birds were given a non-reinforced test trial, conducted in an arena of the same shape but with walls twice the original length. The outcome of this test revealed searching was concentrated at the centre of the larger test arena. Such behaviour is not restricted chicks. When tested under similar conditions to those just described, both pigeons (Gray, et al, 2004) and rats (Tommasi & Thinus-Blanc, 2004) searched at the centre of a large square arena despite being trained to find a goal located at the centre of a smaller training apparatus of the same shape.

One interpretation of the above findings is that animals searched at the centre of the large test arena because they learned to find food by referring to the overall shape of the smaller one during training. In all the aforementioned experiments (Tommasi & Vallortigara, 2000; 2001; Gray et al, 2004; Tommasi & Thinus-Blanc, 2004) there is, however, some evidence to suggest that animals found the goal by referring to local cues as well. For example, during the test trial with the large square arena animals not only searched at its centre but also in a location that was equivalent to the distance and direction of the food from one corner of the smaller training apparatus. It is thus likely that two strategies were employed to find food. One was based on global cues;

the other on more local cues such as the vector between food and one corner of the small square.

One problem with many of the experiments discussed so far is that neither searching at the centre of a landmark array (Spetch at al 1996; 1997) nor at the centre of an arena with a distinctive shape (Tommasi & Vallortigara, 2000; 2001; Gray et al, 2004; Tommasi & Thinus-Blanc, 2004) necessarily implies that such behaviour was under the control of global spatial information. An alterative explanation is that subjects were looking for a point that was farthest from the objects creating the shape, or attempting to equalize their estimated distance from these objects (Tommasi & Vallortigara, 2000). Support for these two alternatives comes from the finding that after being trained to find a goal located at the centre of a square arena, chicks (Tommasi & Vallortigara, 2001) and rats (Tommasi & Thinus-Blanc, 2004) will also search at the centre of a triangular arena (of approximately the same area as the original apparatus).

One method of overcoming the above problem is to train animals to find a goal located in one corner of a shape created by a set of objects and several authors have done just that (Kelly & Spetch, 2001; Tommasi & Polli, 2004; Pearce et al, 2004; Esber et al, 2005). One such experiment was conducted by Kelly and Spetch (2001) who trained pigeons to find food that was hidden in one corner of a rectangular arena: the correct corner. All four walls of the arena were white and four identical landmarks occupied each corner. Due to the absence of distinctive features, the rectangle thus described the location of food ambiguously. By the end of training, pigeons searched the correct and the geometrically equivalent corners with equal frequency. Moreover, they successfully discriminated these corners from the remaining incorrect corners of the arena. An identical pattern of results was obtained during a non-reinforced test trial conducted in an arena that was indistinguishable from the training apparatus. Pigeons thus seemed to have used the overall shape of the arena to find food.

Further evidence in support of the above claim is provided by the results of two transformation tests. The first took place in a medium sized rectangle, the ratio between the lengths of its walls being the same as the original apparatus. The outcome of this test revealed that the preference exhibited by pigeons for the two geometrically correct corners did not differ from that obtained during the first test trial. However, when tested in a square arena pigeons showed an equal preference for each corner. On the basis of these results Kelly and Spetch (2001) argued that pigeons must have found food by referring to the overall shape of the rectangular arena.

There are, however, two good reasons to be suspicious of the above claim. First, Kelly and Spetch (2001) only ever tested pigeons in arenas that were either the same size or smaller than the original one. Smaller arenas are relatively insensitive for detecting the use of competing way-finding strategies. It thus remains a possibility that pigeons searched with reference to local as well as global cues. A rectangular environment larger than the training apparatus would have provided better circumstances for testing and it is perhaps only under these conditions that the use of non-geometric strategies for searching might have been revealed.

Another piece of evidence to suggest that navigation may not have been under the control of global cues is that during a test without food and conducted in an arena with sides half the original length, pigeons' preference for the geometrically correct corners did not exceed that expected by chance. Had navigation been based on global cues then subjects should have searched corners of the smaller arena that were geometrically equivalent to the one occupied by food during training. No such preference for these corners was exhibited. To account for these latter findings Kelly and Spetch (2001) have argued that pigeons found it difficult to perform in very small environments. Whilst there may be some merit to this explanation it does nothing to elucidate the mechanisms underlying navigation.

One clear conclusion to draw from Kelly and Spetch's (2001) study is that using an arena of the same shape for training and testing makes is difficult to assess whether navigation was under the control of local or global cues. One study to circumvent this problem was undertaken by Pearce et al (2004). The experiment was identical to the one undertaken by Esber et al (2005) except that solid walls were used to create the rectangular and kite-shaped pools. As before rats were trained first to escape from a rectangular pool by finding a submerged platform located in one of its corners: the correct corner. For Stage 2 the platform occupied the right-angled corner of the kite that was congruent with the correct corner. Despite this transformation rats searched in the congruent corner of the kite, which implies they found the platform by using local rather than global cues of the original apparatus.

According to Pearce et al (2004) there are at least three ways in which rats could have found the platform, none of which credits them with having any knowledge of the overall shape of the environment. One possibility is that they used the relationship between the long and short walls to search. As an alternative, rats may have searched by first identifying a short wall, for example, and then headed towards the corner at its right-hand end. Finally, it is plausible that rats developed a habit of turning in a particular direction upon being released from either a long or short side which enabled them to find the platform. In favour of the latter explanation Pearce et al (2004) found that when released from the short side of a rectangular pool, rats habitually turned left which led them to the platform. By comparison, long-side releases resulted in rats turning left or right. It is unlikely, however, that such release-habits are able to fully explain the ability of rats to find the submerged platform in the above studies. Esber et al (2005), in the study mentioned earlier, showed that when for the first time rats were released from the centre of the rectangular array; they nonetheless found the platform which implies they had some other strategy at hand for finding the platform such as searching at a particular end of a short side.

The use of local cues for navigation is also evident in a study conducted by Tommasi and Polli (2004). They trained chicks to find food hidden in one corner of a parallelogram-shaped arena. For one group the correct corner, containing food, always had the short wall to the right of the long wall, its internal angle being 60°. Chicks could thus use corner-angle and the ratio between the long and short walls as cues to find food. Alternatively they might search with reference to the overall shape of the apparatus. To distinguish between these possibilities Tommasi and Polli gave subjects a number of non-reinforced test trials during which the shape of the original apparatus was transformed. Chicks were tested first in a rectangular arena- making it impossible for them to search with reference to either global cues or corner-angle.

Even so, chicks searched corners of the rectangle that were congruent with the correct corner of the parallelogram; an outcome which suggests they used wall-length ratio as a cue to find food.

Chicks were also tested in a rhombus-shaped environment which once again made global cues irrelevant. In addition, given that the sides of the rhombus were the same length it was impossible for chicks to use wall-length ratio as a cue for searching. Despite this change in shape, the corners of the rhombus had internal angles identical to that of the parallelogram. Thus, had navigation been based on corner angle then chicks might be expected to search corners of the rhombus congruent with correct corner of the parallelogram. The results of the test trial confirmed this prediction. Taken together the results supplied by Tommasi and Polli (2004) provide little evidence to suggest that chicks based their search for food on the overall shape of the parallelogram. Instead they seemed to navigate with reference to cues more local to the goal. One effective cue for searching was the angle subtending the correct corner; another was the ratio between the long and short walls.

In summary, Cheng (1986) Gallistel (1990) have claimed that animals should find their way to a hidden goal by referring to the overall shape of the cues which surround it. However, only a modest number of studies lend support to this point of view (Tommasi & Vallortigara, 2000; 2001; Gray et al, 2004; Tommasi & Thinus-Blanc, 2004). In contrast, many experiments suggest that animals navigate with reference to local cues and there are numerous situations in which they do so (Collett et al, 1986; Roberts & Pearce, 1998; Biegler & Morris, 1993; 1999; Spetch & Wilkie, 1994; Garrad-Cole et al, 2001; Spetch et al, 1996; 1997; Esber et al, 2005; Pearce et al, 2004; Tommasi & Polli, 2004). The latter findings thus go some way to undermine ideas expressed in the theory of the Geometric Module (Cheng, 1986; Gallistel, 1990) whilst at same time lend support to elemental theories of associative learning like the Rescorla-Wagner model (1972). They also raise the possibility that local rather than global cues guided rats to the platform in all 8 of the previous experiments. If there is any merit to the latter idea then it would imply that the featural cues used in those experiments failed to restrict spatial learning based on local cues rather than on the overall shape of the test apparatus. The conclusions drawn from Part I would then need some revision. Further discussion relating to this issue shall be reserved to until the results of the next experiment.

5.06.

Experiment 9

Experiment 9 was designed to test the proposal made by Cheng (1986) and Gallistel (1990) that animals should identify the position of a hidden goal by referring to the overall shape of the cues surrounding it. To this end, two groups of rats were trained first to escape from a circular pool onto a submerged platform that was located in one corner of the virtual rectangle used for Experiment 4. Throughout Stage 1 the platform always occupied a corner with the same geometric properties. It might have been positioned, for example, in either of the two corners with the long side to the right of the short side. To be consistent with previous experiments the corner with the platform was always considered to be the correct corner and was labelled A. Corner C was the geometrically equivalent corner and the remaining incorrect corners were B and D respectively (see figure 5.02).

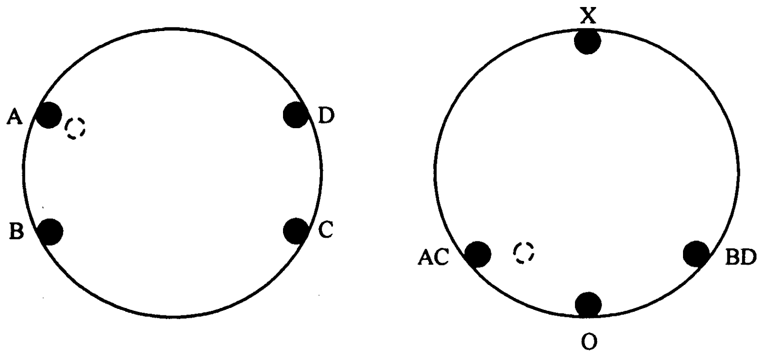

Figure 5.02. The arrangement of apparatus used for Experiment 9. The filled circles denote the cylindrical landmarks. The dashed circle shows the position of the submerged platform. Stage 1 was undertaken in the rectangle (left-hand side) and Stage 2 in the kite (right-hand side). Corner AC was congruent with corners A and C, but incongruent with corners B and D. Corners O and X were the obtuse angled corner and the Apex corner, respectively.

After sufficient training, upon being released into the pool rats were expected to swim either directly to the corner containing the platform or the geometrically equivalent corner from where they would then head to the correct corner (McGregor et al 2004).

Throughout the first stage the pool was surrounded by a curtain and the orientation of the rectangle with respect to the experimental room was changed for each trial. Moreover, even though the four cylinders were identical their relative positions in the array were varied randomly from trial to trial. These steps were taken in order to prevent subjects from finding the platform with reference to cues outside the pool, or any local cue within the pool provided by the walls of the pool itself or indeed by a feature on any of the four landmarks. As a result, successfully discriminating between the correct and incorrect corners should depend upon information supplied by the arrangement of four cylinders, but not by any other cue either inside or outside the pool.

To assess whether rats had learned to discriminate between the correct and incorrect corners of the rectangle they were given a test trial during which the platform was removed from the pool. Evidence of a successful discrimination would then be revealed by rats exhibiting a greater preference for swimming in the correct and geometrically equivalent corners, than for swimming in the remaining incorrect corners of the pool.

To examine whether this discrimination was based on local or global cues of the rectangle, for the second stage of the experiment the cylinders were rearranged into the shape of a kite (see figure 5.02, right-hand side). Corners at AC and BD were both right angled, and the lengths of the short and long sides in the kite-shaped array were the same as those in the rectangular array. Corner AC in the kite was thus geometrically equivalent to corners A and C in the rectangle. Similarly, corner BD was congruent with corners B and D because they shared the same geometric properties. The remaining corners in the kite were the obtuse angled corner (O) and the apex (X). For Group Congruent the platform occupied the corner in the kite with the same geometric properties to the corner containing the platform in the rectangle. Thus, if the platform occupied corner A in the rectangle, it was placed in corner AC of the kite. For Group Incongruent the corners with the platform in the two shapes differed, geometrically. If placed in corner AC in the rectangular array, then the platform occupied corner BD in the kite.

If rats identified the position of the submerged platform by referring to the overall shape described by the four cylinders, then the difference between the two arrays should mean that the effects of training during Stage 1 would be of little use for finding the platform in Stage 2. Alternatively rats may have found the platform by referring to more local information associated with the arrangement of landmarks in Stage 1. If this is the case, the behaviour of rats in the kite-shaped array might be influenced by their prior experiences with the rectangular array. According to Pearce et al (2004) one method suitable for finding the platform in Stage 1, for example, would have been to search in a corner of the rectangular array with the short side to the left of the long side. If rats relied on such local geometric information then the groups in the second stage should show a preference for searching in corner AC rather than corner BD which would assist Group Congruent to find the platform in the kite but hinder Group Incongruent. Alternatively, rats could have used the much simpler non-geometric strategy of heading to the right-hand end of a short side (or left-hand end of a long side) of the rectangle in Stage 1 (see Pearce et al, 2004). The use of either of these methods for searching would facilitate the performance of Group Congruent during conditioning trials with the kite, but disrupt that of Group

Incongruent.

Method

Subjects and Apparatus The 20 rats were of the same stock, with similar experience, of approximately the same age, and housed in the same conditions as those from the previous experiment. At the start of the experiment the rats were assigned randomly to two groups of equal number. Four black cylinders, identical to the ones used in the Experiment 4 were used to create two virtual shapes. The first shape was rectangular and was identical to that of Experiment 4, whilst the second was a kite which is depicted in figure 5.02. For both shapes the long sides were 1.8 m and the short sides were 0.9 m. Referring to figure 5.02, cylinders at corners X and O were always placed on the diameter of the pool, which ensured that the corners of the kite shape created by the other two cylinders were both right angled. The centre of the platform was located 30 cm from the centre of the cylinder located at the appropriate corner, on a line that bisected the corners at AC and BD. Throughout the experiment the curtain was drawn around the pool, to occlude any extraneous cues in the experimental room.

Procedure In each of 16 sessions of training with the rectangular array the groups were required to escape from the pool by swimming to a submerged platform. For each group the platform was located in one corner of the rectangular array defined by the four cylinders. For half the subjects of each group the platform was placed in the corner with the short side to the left of the long side, whilst for the remaining subjects it was in the opposite corner. Within a session, the platform was located twice in each geometrically equivalent corner of the pool, in a random sequence. The centre of the platform was 30 cm from the closest edge of the nearest cylinder on an imaginary line that bisected geometrically equivalent corners of the rectangle. For the four trials in each session each rat was released once, in a random sequence, from start points that were located on the edge of the pool at North, South, East and West. Rats were lowered into the water facing the wall of the pool. Following each trial the virtual rectangle was rotated either clockwise or anticlockwise so that the midpoint of the imaginary line created by cylinders A and B was located on the North, East, South or West points of the pool's edge. For the purpose of the experiment North was considered to be opposite to entrance of the experimental room. The rectangle could move through more than 90° between each trial and the sequence of rotations was varied randomly for each session.

The first three trials of Session 16 were conducted in the manner described above. For the final trial of this session a test was conducted during which the platform was removed from the pool. For the duration of the test the imaginary line bisecting the rectangle's length was oriented along the East-West axis of the pool. Rats were released from a novel point located at the centre of the pool and were allowed to swim freely for 60 s. After the test subjects were led to one of the corners where the platform had previously been located and removed from the pool. The path taken by rats during the test was recorded using Watermaze software (Morris & Spooner, 1990). For the purpose of this measurement the pool was divided into four quadrants of equal area and the time rats spent in each quadrant was recorded. It must be noted that the quadrants extended beyond the boundary of the virtual rectangle to the edge of the pool. A rat was regarded as searching in the correct quadrants of the pool whenever it entered the quadrant previously occupied by the platform and its geometric equivalent.

Subsequent to the test trial subjects received two further training sessions with the rectangular-shaped array which were conducted in an identical manner to all other training trials with this apparatus. Stage 2 training used the same four black cylinders as the previous stage, but they were arranged in a kite rather than rectangular configuration. There were 3 sessions in the final stage, each comprising four trials for which rats were required to find a submerged platform located in one right-angled corner of the kite. For half the rats in each group the platform was located in corner AC, whilst for the remaining half it occupied corner BD (see figure 5.02). For Group Congruent, the geometric properties of the corner containing the platform in the kite were identical to those of the correct corner in the rectangle.

To avoid rats using unintended cues, the kite-shaped array was rotated either clockwise or anticlockwise for each trial. To achieve this, the cylinder at corner X was located on the North, South, East and West points at the pool's edge and the relative positions of the remaining three cylinders were changed accordingly. The kite could move through more than 90° in one rotation between trials with the constraint each compass point was used at least once in each session. In addition the sequence of rotations varied in a random sequence for each session. Rats were released from four release points with their snouts facing the wall of the circular pool. These points were located at the edge of the pool in positions that were equidistant from two adjacent landmarks. The cylinders were interchanged with each other in a random sequence and the curtain was always drawn around the pool.

As well as noting escape latencies, in each stage of the experiment a record was taken of the corner a subject first entered after being released into the pool. The method for recording these data was the same as that used in Experiment 4.

Results and Discussion

The group's mean escape latencies from the first 16 sessions during Stage 1 with the rectangular array are shown in figure 5.03. Generally escape latencies declined for each group as the sessions progressed and between group differences were not apparent. A mixed two-way ANOVA of escape latencies over the 16 sessions for the groups showed a main effect of session, $\underline{F}(15, 270)= 24.5$, Mse= 24.46, $\underline{p}= 0.00$, $\eta_p^2= 0.58$, but the main effect of group ($\underline{F}(1, 18)= 0.24$, Mse= 497.83, $\underline{p}= 0.63$, $\eta_p^2=0.02$) and the interaction of Group x Session were not significant ($\underline{F}(15, 270)= 0.86$, Mse= 200.60, $\underline{p}= 0.61$, $\eta_p^2= 0.05$)

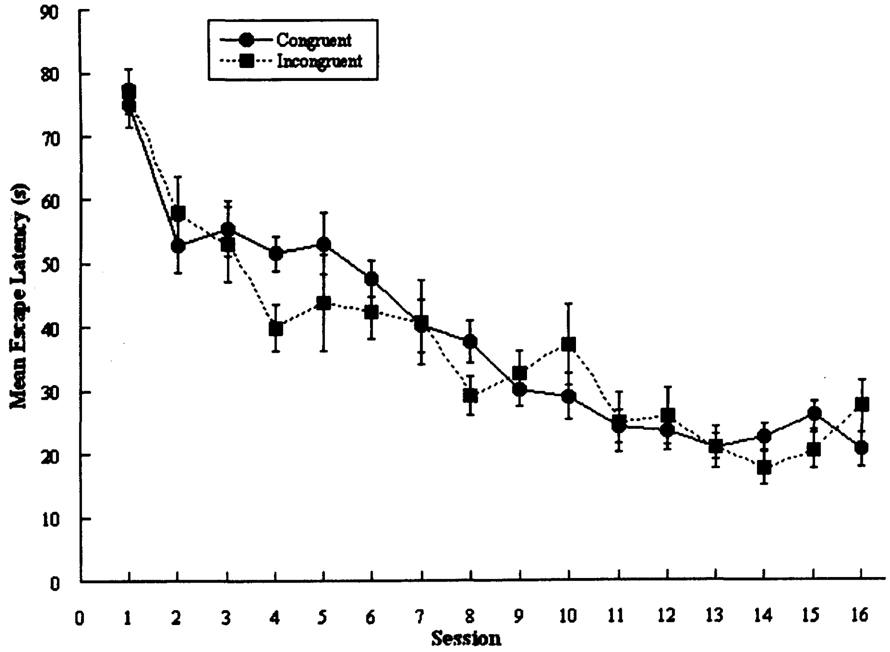

Figure 5.03. Mean escape latencies for the groups during Stage 1 of Experiment 9 (error bars represent ±1standard error of the mean).

Figure 5.04 shows the mean percentages of trials on which the groups entered first each corner of the rectangular pool during Stage 1. There was little difference between the performances of the Groups, except during session 5 where Group Incongruent (right-hand panel) spent more trials than the Group Congruent (left–hand panel) searching the corner of the rectangle occupied by the platform. Generally both groups learned to search for the platform in the correct and the geometrically equivalent corners and there were few occasions, especially towards the end of training where the groups searched corners B and D first.

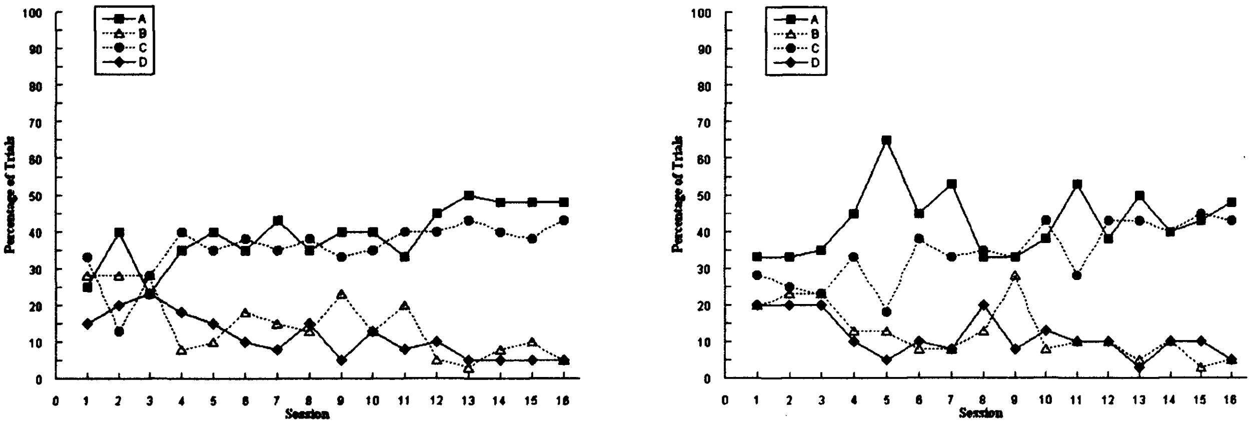

Figure 5.04. Mean percentages of trials that Group Congruent (left-hand panel) and Group Incongruent (right-hand panel) entered first each corner of the rectangular array during Stage 1 of Experiment 9.

To assess whether the groups discriminated the geometrically correct corners from the incorrect corners of the pool, for each subject the mean percentage of trials they swam to each to the four corners was calculated for the 16 sessions combined. For the correct corner of the pool (A), the geometrically equivalent corner (C) and Corners B and D respectively, these percentages were: 38, 36, 15 and 12 for Group Congruent; and 43, 33, 12 and 12 for Group Incongruent. Within group comparisons revealed that Group Congruent entered the correct and geometrically equivalent corners equally often (T(10)=31). This group entered first each of corners A and C significantly more often than the two remaining incorrect corners of the pool (Ts(10)=0). Similar comparisons showed that Group Incongruent spent more trials searching for the platform in corner A than C. Given that the groups were treated identically during Stage 1, there is no obvious reason why Group Incongruent should have exhibited such a bias. This group nevertheless entered first each of corners A and C significantly more often than corners B and D (Ts(10)=0). Together these results confirm the groups successfully discriminated the geometrically correct corner from the incorrect corners of the pool, which implies rats used the shape of the rectangular array to find the platform.

The above percentages were also used to compare the performance of the groups. Between group comparisons revealed that the groups entered first each corner of the pool equally often, Us (10, 10) ≥38≤81. It is thus unlikely the bias Group Incongruent had for searching corner A over C, would have any impact on the results of the test trial conducted with the rectangular array or conditioning with the kite-shaped array during Stage 2.

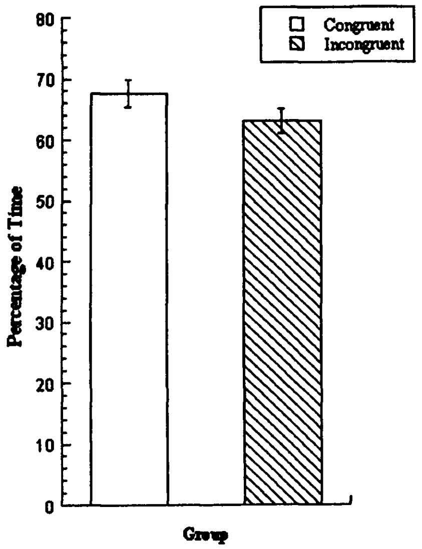

Figure 5.05. Mean percentages of time the groups spent searching in the correct quadrants of the rectangular array during the test without the platform and landmark (error bars represent ±1 standard error of the mean).

During the final trial of session 14 rats were given a test with the rectangular array but in the absence of the platform. This test was conducted to assess the extent to which rats used the cues provided by the rectangle to find the platform. Figure 5.05, shows the mean percentages of time that rats swam in the correct quadrants of the pool during the 60-s test trial. The figure shows that both groups expressed a clear preference for searching in the geometrically correct quadrants. One sample t-tests confirmed that both groups spent significantly more than 50% of their time in the correct quadrants. These results were: t(9)=8.88, p=0.00, for Group Congruent; and t(9)=5.63, p= 0.00, for Group Incongruent. A one-way ANOVA of the time the groups spent in the correct quadrants of the pool showed that between group differences were absent F(1, 18)= 0.20, Mse=50.78, p=0.66, η_p^2=0.01. These results provide further evidence in support of the idea that rats used the cues provided by the rectangular array to find the platform.

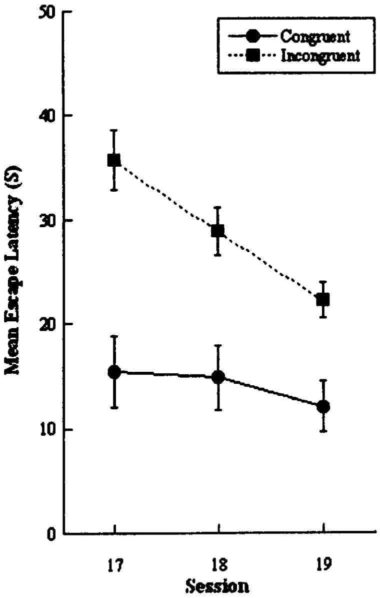

Figure 5.06. Mean escape latencies for the groups during Stage 2 of Experiment 9 (error bars represent ±1standard error of the mean).

The group's mean escape latencies for acquisition trials from the final 3 sessions of the experiment can be seen in figure 5.06. The figure shows that escape latencies declined for each group as the sessions progressed. From the outset and throughout the final sessions of training Group Congruent was always quicker to escape onto the platform than Group Incongruent. A mixed two-way ANOVA of escape latencies over final 3 sessions for the groups, revealed a significant main effect of group, $\underline{F}(1, 18)=71.48$, Mse= 45.80, $\underline{p}= 0.00$, $\eta_p^2= 0.80$, a main effect of session, $\underline{F}(2, 36)=6.38$, Mse= 55.68, $\underline{p}= 0.00$, $\eta_p^2=0.$ but the interaction of Group x Session, $\underline{F}(15, 270)=2.32$, was not significant. Had searching for the platform been based on the overall shape of rectangle in Stage 1, then both groups would have found it difficult to escape from the pool in the kite during Stage 2. Instead the performance of Group Congruent was superior relative to Group Incongruent, which suggests that rats based their search for the platform on local cues associated with the rectangle.

A record was also taken of which corner a rat first entered after being released into the kite-shaped array. To keep the following analyses as simple as possible it has been assumed that all animals were trained with the platform in corner A of the rectangle. Hence, corner AC of the kite was considered to be geometrically correct, even though this corner did not contain the platform for Group Incongruent.

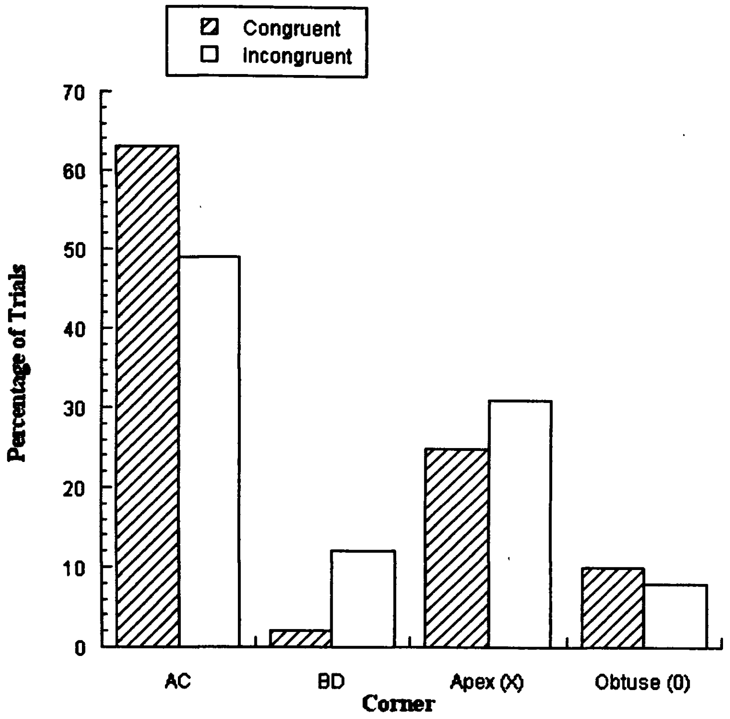

Figure 5.07. Mean percentages of trials that the groups entered first each corner of the kite-shaped array during Stage 2 of Experiment 9

Figure 5.07 shows which of the four corners of the kite-shaped array each Group entered first after being released into the pool. For Group Congruent entries to corner AC were considerably greater than for any other corner of the pool including the other right-angled corner where rats rarely searched. This group also showed a bias for searching the corner at the apex of the kite. A similar pattern of results was observed for Group Incongruent. They also swam to corner AC more often than any other corner as well as displaying a preference for the corner at the apex. There were very few occasions on which Group Incongruent searched the corner BD.

To assess the above observations the mean percentages of trials on which corners AC, BD, X and O were entered first by each group for the 3 sessions combined were calculated. These percentages were: 63, 2, 25, and 10, for Group Congruent and; 49, 12, 31, and 8, for Group Incongruent. Within group comparisons revealed that Group

Congruent entered first corner AC significantly more often than each of corners BD, X or O, Ts (10)≤4. In addition rats entered the corner at the apex of the kite (X) more often than each of the obtuse angled corner, O, and the other right-angled corner without the platform, BD, Ts(10)≤5. Finally, Group Congruent entered first the obtuse angled corner more frequently than corner BD, T(10)=0. Group Congruent thus showed a significant preference for searching X, albeit to a lesser extent than their preference for Corner AC.

Similar comparisons revealed that Group Incongruent entered first corner AC significantly more frequently than each of corners BD and O Ts(10)=1. These rats swam first to corners AC and X, equally often T(10)=10. The latter corner was entered first significantly more often than either corners BD or O, Ts(10)=0. The difference between the latter two corners was not significant T(10)=10. These results confirm that rats showed an equally strong bias for swimming first towards corners AC and X.

One unexpected outcome from the experiment is that rats exhibited a pronounced bias for searching two corners of the kite. The first, corner AC, was congruent with the one that contained the platform in the rectangle. The second was the apex of the kite. Such findings make it unlikely that rats found the platform by referring to the overall shape of the rectangle. Had they done so, then Stage 1 training should have failed completely to influence performance in the kite. Rats nevertheless successfully discriminated the two right-angled corners of the kite. Their behaviour may have therefore been under the control of local cues, several of which were summarised in the introduction to this chapter.

One possibility is that rats found the platform in the rectangle by swimming toward the correct corner, which was right-angled. However, had rats also relied on this method to find the platform in Stage 2 then they would have restricted their searches to corners AC and BD, because these were the only right-angled corners in the kite. Alternatively, rats may have used wall-length ratio as a cue to find the platform, by swimming to a corner of the rectangular array with the long side to the right of the short side. This latter method would have ensured rats swam to corner AC on every trial that they were released into pool when the four landmarks were rearranged to form the kite, but it fails to explain why rats also showed a bias for corner X and why they failed to enter BD. A third method for escaping from the pool during Stage 1 would have been to identify first a short side of the rectangle and then head towards its right-hand end, which if used in kite would guide rats to corners AC and O, but no other corner: which once again neglects to account for the bias rats had for corners AC and X. Finally, rats may have identified first one of the rectangles long side's and then swam towards its left-hand end, a method which would have led rats to search corners AC and X in the kite. The final method thus provides one way to account for the bias rats displayed for searching the corner of the kite containing the platform as well as the corner at the apex. One shortcoming of the latter method, however, is that it fails to explain why Group Congruent had a bias for searching the obtuse angled corner over corner BD. It is apparent then that none of the aforementioned searching-strategies explains fully the behaviour of rats in the kite. Rats must have thus had some other method for finding the platform that did not require the use of local or global geometric cues.

One explanation for the preference rats had for swimming to corners AC and X in the kite is that they found the platform in the rectangle by turning in a particular direction upon being released into the pool. During Stage 1 rats were released from the middle of either the long or short sides of the rectangle. Assuming that the platform occupied corner A, then turning left after being released from a short side would have ensured rats headed to a geometrically correct corner. Likewise they would consistently approach a geometrically correct corner if they turned right upon being released from a long side. Performing such simple response-habits would thus have ensured that animals succeeded in swimming toward a geometrically correct corner on every occasion they were released into the pool.

Both groups swam first to the geometrically correct corners (A & C) on 90% of trials in the final session of training with the rectangular array and over half of subjects did not make any errors of searching the remaining corners. Simply turning in a particular direction upon being released into the rectangular pool can thus explain the accuracy rats achieved for searching the geometrically correct corners. The question is then raised "did rats use such response-habits to search when the four landmarks were rearranged to form the kite in Stage 2?"

One way to answer the above question is to compare the mean percentages of trials rats entered first each corner of the kite, with the percentages of trials they would be expected to search in those corners if they had used the response-habits advocated above.

Assuming that in the kite rats adopted the strategy of turning left when released from a short-side, and of turning right when released from a long-side; the predicted percentages for searching in corners AC, BD, X and O would be 50, 0, 25 and 25, respectively. These figures mimic the general pattern of results obtained for training in the kite-shaped array and show that corner AC would be preferred over any other corner, with entries to corner BD being rare. The above scheme also explains the preference Group Congruent had for swimming toward corner O over corner BD, but cannot account for the absence of this preference in the other group. In addition, according to the above figures rats would be expected to search equally often in corners X and O. In reality rats searched more frequently in the former than in the latter corner. Perhaps corner X had unconditioned properties that encouraged rats to swim more frequently to that corner rather than the corners at the base of the kite. One obvious difference between the apex and the two remaining corners of the pool was its acute angle which may have prompted animals to explore it. The predictions above are therefore somewhat imperfect. It is worth pointing out, however, that no other permutation of turning in a particular direction upon being released from either a long or short side comes close to approximating the observed values. With this thought in mind, it is not unreasonable to suppose that searching for the platform in the kite was guided by the same response-habits that guided rats to the platform in the rectangular array.

From a sceptical point of view it could be argued that evidence to show rats adopted a strategy of turning in a particular direction to find the platform is rather weak. There may be some merit to such a criticism. To begin with, one limitation of Experiment 9 was that it was not possible to classify which corner a rat first entered in terms of which side it was released into the rectangular and kite-shaped arrays because a record was not kept of which side of the pool rats were released from and only the corner a rat first entered upon being released was recorded. It retrospect it would have been more prudent to record on every trial every corner a rat entered until the platform was found. Unfortunately these measures were not taken. Even so, there is at least one other experiment, conducted in the same laboratory, with the same apparatus and using the same design as Experiment 9, that provides firm evidence to show the use of stereotypical turning responses by rats to find their way to a hidden platform (Esber et al, 2005). In that study two groups of rats were trained first to find a platform situated in one corner of a rectangular and then the kite-shaped array. For Group Consistent the platform occupied a corner of each shape comprising the same geometric properties. The platform occupied corners with different geometric properties for Group Inconsistent. Esber et al recorded on every trial the sequence of corners that rats entered after being released into the rectangular and kite-shaped pools. Because they also kept track of whether rats were released from a long or short side it was possible to determine if subjects had a bias for turning in a particular direction upon being released into the pool. The results provided by Esber et al (2005) show that rats acquired a tendency of turning left or right when released from a long side of the rectangular apparatus, and of turning left upon being let go from one of its short sides. These tendencies for turning in a particular direction were once again observed in the kite-shaped array. Finding the platform in the kite thus appears to have little to do with the use of local or global geometric cues provided by the rectangular shaped array. Instead searching was based on a response-habit, a finding which is entirely consistent with the results of Experiment 9. Of course the preceding arguments are based on comparisons across experiments and therefore need to be taken with the usual manner of caution.

5.07.

General Discussion

Contrary to predictions that can be derived from the theory of the Geometric Module (Cheng, 1986, Gallistel, 1990) the results of Experiment 9 imply that rats did not refer to the overall shape of the rectangular array to find the platform. In support of this conclusion both groups exhibited a strong preference for searching the corner of the kite that was congruent to the one that contained the platform in the rectangular array. Given the difference between the two shapes, it is thus logical to conclude that rats used a method for searching that did not rely on the overall of the appartus.

One surprising finding from the experiment is that rats also displayed a preference for searching the corner at the apex of the kite. Such results are once again difficult to explain in terms of the Geometric Module theory (Cheng, 1986; Gallistel, 1990), the application of which predicts that rats should have failed to exhibit a preference for all four corners of the kite-shaped array.

The suggestion was made earlier that the bias rats had for swimming towards the congruent and the apex corners of the kite could not be explained in terms of them using local geometric cues. Instead rats may have found the platform by simply turning in a particular direction upon being released into the pool. Such response-habits would have guided rats to the correct and geometrically equivalent corners on every trial conducted with the rectangular array. Moreover, if these response-habits transferred to the kite-shaped array then rats would be expected to show a preference for the congruent and apex corners, which is exactly what the results of the experiment revealed.

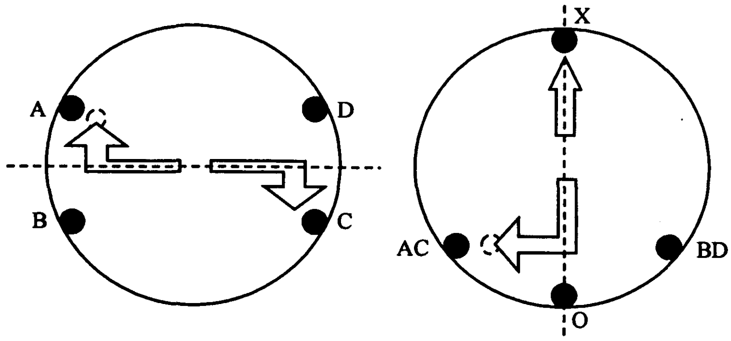

Figure 5.08. The apparatus used in Experiment 9. The principle axes of the rectangular and kite-shaped arrays are given by the dashed lines. The arrows depict which corners rats should search if they swam to the extreme right-hand end of each principle axis.

Even though it seems unlikely that generalisation between the rectangular and kite-shaped arrays was not mediated by the congruence between them; Cheng and Gallistel (2005) have argued that the transfer of behaviour may have, nevertheless, been based on a global spatial cue. According to Cheng and Gallistel one possibility is that during their training rats found the platform by first identifying the principle axis of the rectangular array. The principle axis, or long axis, passes through the centroid of the shape (see figure 5.08). Assuming that the platform was located in the corner with the long side to the right of the short side, rats may have escaped from the pool by searching for a corner positioned to the extreme right of the principle axis. Relying on this method for finding the platform would ensure that rats searched the correct and geometrically equivalent corners of rectangular array on the majority of trials. If rats persisted in using the same method for searching when transferred to the kite-shaped array then they would be expected to show a bias for the correct and apex corners, which corresponds to the general pattern of results observed in Experiment 9.

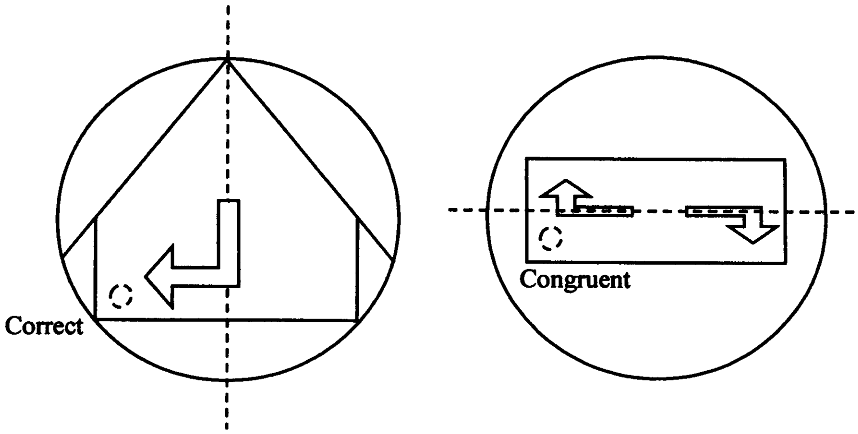

Figure 5.09. The apparatus used by McGregor, Jones, Good & Pearce (2006). The pentagonal pool is shown on the left-hand side and the rectangular pool on the right. The platforms are given by the dashed circular line and the principle axes by the straight dashed lines. The arrows depict which corners rats should search if they swam to the extreme right-hand end of each principle axis.

Referring to the principle axis, however, fails to explain why Group Congruent also exhibited a preference for the obtuse angled corner, over corner BD, rather than just the correct and apex corners. Cheng and Gallistel's (2005) ideas are also difficult to reconcile with the results of a study conducted by McGregor, Jones, Good and Pearce (2006) who trained rats to find a submerged platform located first in one corner of a irregular pentagonal swimming pool and then a regular rectangular pool, each having enclosed walls (see figure 5.09). It is worth noting that the short and long walls at the base of the pentagon were the same dimensions as the corresponding walls of the rectangle. For simplicity it shall be assumed that for every animal the right-angled corner of the pentagon with the short wall to the right of the long wall contained the platform and was considered to be the correct corner. Two Groups were included in the experiment. For Group Consistent the platform in Stage 2 occupied the corners of the rectangle that were congruent with the correct corner. For Group Inconsistent the incongruent corners contained the platform. According to Cheng and Gallistel (2005) rats should, in Stage 1, escape onto the platform by swimming towards the corner at the extreme right-hand end of the principle axis, which extends from pentagon's apex and is perpendicular to and bisects its base. Swimming to the corner at the right-hand end of the rectangular pool's principle axis, however, would lead rats to search corners with the short wall to the right of the long wall, which would help Group Inconsistent to find the platform but hinder Group Consistent.

Over the 3 sessions of Stage 2 with the rectangular pool McGregor et al (2006) noted that Group Consistent swam towards the congruent corners more often than Group Inconsistent, an outcome opposite to that predicted by Cheng and Gallistel (2005). Moreover, compared to the inconsistent group, Group Consistent showed a greater preference for the congruent corners during a test trial conducted in the rectangular pool without the platform- results which once again contradict the ideas expressed by Cheng and Gallistel. Interestingly, McGregor et al conducted two further test trials, both in the pentagonal pool and without the platform. In one test the wall at the base of the pentagon was removed and rats' preference for the correct corner was significantly less than in another test when this wall was present and the pentagon remained intact. Both tests did nothing to modify the principle axis of the environment. It is thus likely that rats based their search for the platform on local cues associated with the correct corner rather than on global cues to do with either overall shape of the apparatus or their principle axes. Such conclusions are of course entirely consistent with the general pattern of results observed in Experiment 9.

One limitation of Experiment 9 is that it was not possible to classify which corner rats first swam to in terms of which side of the two arrays they were released from. Accordingly it could be argued that the evidence in favour of rats developing a response-habit to find the platform is rather circumstantial. There may be some weight to such a criticism. However, the preference for searching in the congruent and apex corners of the kite corresponds to the expected bias for these corners if it is assumed that rats turned right upon being released from a long side and turned left when they released from a short side. Crucially, there is no other combination or permutation of turning in a particular direction upon being released from the long or short sides of the apparatus that approximates the pattern of results provided by the training trials with the kite. It is perhaps worth pointing out that other experiments to use the same design as Experiment 9 have also found that rats tend to use response-habits to find a hidden platform (see Esber et al, 2005; Pearce et al, 2004).

Such response-habits, however, are unlikely to provide a complete explanation for the ability of rats to find the platform in the above experiments. Toward the end of Stage 1 training tests were conducted during which subjects were released for the first time from the centre of the rectangular array in the absence of the platform. During these tests rats exhibited strong preferences for searching in the two geometrically correct quadrants of the array. They must have therefore had at hand, some strategy other than turning in a particular direction for finding the platform. Unfortunately, the limitations of Experiment 9 make it difficult to judge what this strategy might have been.

Subjects may not have even treated the cylinders as having sides per se. They may have merely searched for two or three cylinders relatively close together and then headed for one cylinder on the right or left according to their previous training (Esber et al, 2005). The only clear conclusion that can be drawn from the current experiment then is that searching must have been based on local cues but not on global cues associated with the landmark array.

Before leaving this discussion, it is perhaps worth reconsidering other experiments which have purported to show that animals rely on a global representation of a landmark array to find a hidden goal. In one such study, already mentioned, Benhamou and Poucet (1998) trained one group of rats to find a submerged platform, the position of which was fixed relative to three different landmarks. For one group the landmarks created an isosceles triangle, for the other an equilateral triangle. During a test without the platform the latter group spent an equal proportion of time searching in the three geometrically equivalent positions of pool, whereas the isosceles group spent most of its time swimming in the area previously occupied by the platform. At first sight it appears that searching for the platform was based on the shape of the apparatus. Unfortunately, due to the arrangement of the apparatus rats may have inadvertently acquired a response-habit during training which guided their behaviour in the test. It was possible, for example, for the equilateral group to find the platform by simply swimming circuitously around the pool from one landmark to the next. For the isosceles group the platform occupied an area of the pool without landmarks making it possible for them to find platform by swimming away from the landmarks. It is thus possible to explain the findings supplied by Benhamou and Poucet (1998) without making any reference to shape described by the landmark array.

In a rather different task Greene and Cook (1997) required rats to retrieve food hidden on top of 6 out of 24 identical poles, the apparatus being surrounded by a circular arena. The same poles were baited across all trials and rats could identify the location of food by referring to several landmarks situated around the arena. Even when the landmarks were identical, rats limited their search for food to the baited rather than unbaited poles. Accordingly Greene and Cooke (1997) concluded that rats must have used the shape provided by the surrounding landmarks to search the poles with food. The results of Experiment 9 prompt a rather different interpretation of their results. Rats may have adopted a habit of turning in a particular direction upon being released into the apparatus. Alternatively rats may have searched for food by using a subset of the landmarks- selecting two, for example, and heading toward either the left-hand or right-hand side of the landmarks.

In a similar study, Brown and Terrinoni (1996) trained rats to find 4 baits of food hidden among 25 identical poles arranged to form a square matrix. The baited poles also formed a square and together they were moved as a unit, between trials, around the larger matrix. Once 2 baits had been retrieved rats selected the remaining baits from the other two poles with a probability greater than that expected by chance. Brown and Terrinoni (1996) argued that such behaviour resulted from rats acquiring a representation of the geometric pattern created by the baited poles. Other authors have attempted to explain similar studies in the same way (for example, Brown, Zeiler & John, 2001; Lebowitz & Brown, 1999; Brown, DiGello, Milewski, Wilson & Kozak, 2000; Brown, Yang & Digian, 2002). By way of an alternative explanation Olthof, Sutton, Slumskie, D'Adetta and Roberts (1999) have suggested that the movement of a rat as it travelled from a pole containing food to another, might have served as a stimulus that, through trial and error, could have evoked a response of heading toward poles where the probability of heading finding food would be higher rather than lower. It is thus possible to explain all these studies without alluding to the use of geometric representations.

Neither Experiment 9 nor those discussed above, provide sufficient evidence to suggest that animals used the shape of a landmark array to find a hidden goal. It is perhaps more prudent then to explain behaviour that appears to be under the control of an array of landmarks in terms of local rather than global cues, which undermines the idea that animals possess a Geometric Module (Cheng, 1986; Gallistel, 1990). If there is any merit to this suggestion then the conclusions drawn from Experiment 4 would be brought into question. In that study an experimental group of rats was trained to find a platform hidden in one corner of a rectangular array where a landmark was also located. During a test trial without the platform and landmark, rats searched in the geometrically correct corners of the pool, which suggested that the landmark failed to restrict spatial learning based upon the shape of an array. Of course this interpretation of the results relied on the assumption that animals found the platform by referring to the geometry of the array, an idea that was strengthened by animals making errors of swimming to the geometrically equivalent corner during training. As Experiment 9 shows, however, such behaviour could have been controlled by a variety of other cues, such as turning in a particular direction upon being released into the pool. If rats used a similar method to find the platform in Experiment 4, then it would imply that the presence of the landmark failed to restrict learning based on local cues rather than on spatial learning based on the overall shape of the test apparatus- which would then undermine further the proposals made by Cheng (1986) and Gallistel (1990).

Whether it is necessary to offer similar explanations for behaviour that appears to be under the control of an environment with enclosed walls, such as those used in the previous chapters remains uncertain. Such explanations certainly cannot be ruled out. However, even if it is assumed that rats used local rather than global cues to find the platform in every one of my experiments, a suitable explanation for the repeated failures to find cue competition would still need to be sought. Perhaps the kind of release habits exhibited by rats in Experiment 9 capture behaviour rather easily which prevented other cues such as landmarks from acquiring any control over searching the platform. Although intuitive such an explanation is ill-defined. As an alternative Miller and Shettleworth (2007) have recently described an associative theory, based on the Rescorla-Wagner model (1972), which may explain why learning based on the shape of an environment is unaffected by the presence of landmarks and this is considered in the final chapter.

6.01 General Discussion

The overall purpose of the nine experiments was to assess the theory of the Geometric Module (Cheng, 1986; Gallistel, 1990). According to that theory animals should navigate with reference to a representation of the overall shape of an environment which is stored in a dedicated geometric module, impenetrable to featural information. It thus follows that competition should not be observed between the shape of an environment and any featural cue placed within it. Moreover, animals should find their way to a hidden goal by using the cues surrounding it in a global rather than local fashion. The ideas expressed in the theory of the Geometric Module (Cheng, 1986; Cheng & Gallistel, 1990) thus contravene the general principle of cue competition described by the Rescorla-Wagner model (1972) and other theories of learning such as that proposed by Pearce (1994).

Unfortunately many of the studies conducted to examine the proposals of Cheng (1986) and Gallistel (1990) have been poorly designed which has made it difficult to assess whether featural and geometric cues compete for the control they acquire over behaviour. By comparison, all the experiments included in this thesis were designed with associative learning theories in mind (Mackintosh, 1975; Pearce & Hall, 1980; Rescorla & Wagner, 1972) and care was taken to include the appropriate control groups and the tests necessary to detect the effects of cue competition. Despite these precautions, the first three experiments of Chapter 2 failed to provide any hint to suggest that learning based on a pool with a distinctive shape was overshadowed by a landmark placed within it. Similar results were supplied by Experiment 4, in which four landmarks were used to describe a rectangular pool. Experiments conducted in Chapter 3, extended the generality of these results by showing that cues situated outside a pool failed to overshadow learning based on its shape.

Experiments 2 and 3 provide particularly stringent tests of cue competition because they used blocking rather than overshadowing designs. In each experiment, a blocking group was trained to swim to a platform near a landmark first in one shape and then a different shape. According to the Rescorla-Wagner model (1972) pre-training with the landmark should have blocked (Kamin, 1969) spatial learning based on the shape of the pool in Stage 2. The experiments nevertheless failed to confirm this prediction: the landmark failed to block learning based on the rectangular (Experiment 2) and triangular-shaped (Experiment 3) pools. Such results seem to add weight to the ideas expressed in the theory of the Geometric Module (Cheng, 1986; Gallistel, 1990) whilst at the same time undermine theories of associative learning like the Rescorla-Wagner model.

One way to reconcile the failures to detect cue competition found in Chapters 2 and 3 with associative learning theories (Rescorla & Wagner, 1972) is to assume that the landmark and the room cues were less salient than the shape of pool. If there is any merit to this idea then these featural cues would have failed to acquire sufficient control over behaviour to restrict spatial learning based on the geometry of the pool. Such an assumption, however, deserves little credit. The results from the initial training stages of Experiments 2 and 3 showed there was little difference between the salience of the landmark and that of the rectangular and triangular-shaped pools. Moreover, despite attempting to reduce the salience of environmental geometry in Experiment 4, learning based on the rectangular array was unaffected by a landmark placed in one of its corners. It thus seems unlikely that cue competition was unsuccessful in the first four studies because the landmark was a weaker cue for finding the platform than the shape of the pool. Similarly, it is difficult to explain the failures to find overshadowing in Chapter 3 by referring to the relatively low salience of the room cues compared to the shape of the pool. The results from the training stage of Experiment 6, for example, showed that the room cues were just as salient as the triangular-shaped pool.

One unexpected result from Experiment 6 is that the presence of a triangular-shaped pool potentiated learning based on the room cues. Similarly, the results of Experiment 7 were interpreted as providing evidence to suggest that learning based on the rectangular pool was potentiated by the presence of the landmark above the platform. One implication of these results is that overshadowing and blocking may have occurred in all the previous studies but their effects were counteracted by potentiation. If this analysis is correct, then the previous failures to detect cue competition can be explained in terms of associative learning theory (Rescorla & Wagner, 1972). One weakness to this approach is that it can be used to explain any experimental outcome because it fails to specify the conditions under which overshadowing and potentiation will be observed, and to what degree.

One factor known to influence potentiation is relative stimulus salience. According to Bouton et al (1987) potentiation is normally observed when the salience of the target stimulus is weak and the one accompanying it is of an intermediate salience. Neither

Experiments 6 nor 7 provided circumstances corresponding to those described by Bouton et al (1987) which makes the potentiation observed in those studies surprising and difficult to explain. It is also worth bearing in mind that rats were trained with similar methods and apparatus in every experiment, yet only two resulted in potentiation- not one resulted in cue competition.

One way to explain the occurrence of potentiation has been to refer to the development of between-stimulus associations (Rescorla, 1981). The outcome of Experiment 8, however, makes it unlikely that the potentiation observed in Experiment 7 resulted from associations developing between the shape of the pool and landmark. It is also unlikely that referring to between-stimulus associations could account for the potentiation observed in Experiment 6, primarily due to the distance between the room cues and the triangular-shaped pool. Other experiments to reveal potentiation have, for instance used stimuli presented much closer together in time and space (Durlach & Rescorla, 1981; Pearce et al 2001; 2006; Graham et al, 2006).

An attractive alternative to the above explanation for potentiation, mentioned earlier, is to refer to the acquisition of habits. In Experiment 6, rats were trained to find a submerged platform situated in one corner of a triangular-shaped pool which was surrounded by room cues. For Group Stable the room cues and shape of the pool were relevant for finding the platform whilst for Group Oscillate only the room cues were relevant. Compared to Group Oscillate, Group Stable made fewer errors of swimming to the incorrect corner at the base of the triangular-shaped pool. As a result Group Stable may have developed a greater habit of swimming to the correct corner than Group Oscillate. Transfer of these different habit-strengths to the test conducted in the triangular pool (but in the absence of the room cues) would then explain why Group Stable spent more time searching in the correct quadrant of the pool than Group Oscillate. A similar explanation can account for the potentiation observed in Experiment 7: the presence of the landmark above the platform may have resulted in Group Landmark acquiring a greater habit of swimming to the correct corner of the pool than the control group for which the landmark was absent during training.

Two of my experiments revealed evidence of significant potentiation and several others provided a hint of a similar effect. Thus, learning based on the shape of an environment was superior when the shape of the pool and a featural cue indicated where the platform could be found than when the feature was absent. Given the above arguments such results raise the possibility that the behaviour of rats was guided chiefly by a habit of turning in a particular direction upon being released into the pool, rather than by the geometry of the environment. If this conclusion is correct then it would not only bring into question the proposals of Cheng (1986) and Gallistel (1990) it would also imply that featural cues do not restrict the acquisition of habits by animals as a means of searching for a hidden goal. Instead the presence of a featural cue may encourage animals to develop a habit of turning in a particular direction upon being released into an environment with a distinctive shape. One study which can be used to illustrate this idea was conducted by Graham et al (2006), who trained rats to find a submerged platform in one right-angled corner of a kite shaped pool. The adjacent short and long walls of one right-angled corner were black whilst the two remaining walls were white. For Group Shape-Only the platform remained in the same right-angled corner, but on half of the trials this corner had two black walls and on the remaining half it had two white walls. The shape of the pool was thus relevant for finding the platform and wall colour irrelevant. Over the course of training Graham et al noted that rats swam to the correct corner more frequently when its walls were black than when they were white, which implies they developed a habit of swimming to the black corner first. Thus, the presence of the featural cue, in this case the black walls, seems to have encouraged animals to find the platform by using a habit rather than by referring to the overall shape of the environment. The use of such habits, however, can be prevented. In additional experiment Graham et al trained rats in the manner just described and using the same apparatus as before with the exception that a landmark was placed above the platform. On this occasion rats did not show a bias for swimming toward the corner with the two black walls first. The presence of the landmark thus appears to have prevented rats from developing a habit of heading to the black corner first.

It thus seems difficult to predict when the interaction of two cues will result in potentiation, or in the failure or even success of cue competition. Pearce et al (2001) have shown, for instance, that a landmark above a platform will potentiate learning based on a triangular-shaped pool and a similar effect was observed with a rectangular pool in Experiment 7. Learning based on the room cues in Experiment 6 appears to have been potentiated by the triangular-shaped pool. In other studies the presence of a coloured wall has been shown to potentiate learning based on a kite-shaped pool (see Graham et al, 2006; Pearce et al, 2006), whilst the same cue has overshadowed learning based on a rectangular pool (Pearce et al, 2006). Gray, Bloomfield, Ferrey, Spetch and Sturdy (2005) have also shown that a coloured wall can overshadow learning based on a rectangular arena. In that study mountain chickadees were trained to find food in one corner of a rectangle with enclosed walls. For the experimental group the long wall near the food was blue, the remaining walls white. When tested in an all white arena, these subjects spent fewer trials searching in the corner previously occupied by food than a control group for whom the arena was entirely white during training. There are many differences between these studies and my own which makes it difficult to offer a straightforward explanation for the different results they have provided. However, it is obvious from these studies that learning based on the shape of an environment is sometimes influenced by the presence of featural information, which poses problems for the theory of the Geometric Module (Cheng, 1986; Gallistel, 1990).

Recently Miller and Shettleworth (2007) have described an associative model of geometric learning which, they argue, can explain why the presence of a featural cue can sometimes overshadow, block or even potentiate learning based on the shape of environment. For present purposes only the single choice version of Miller and Shettleworth's (2007) model shall be discussed. It shall be described with reference to a hypothetical experiment in which an experimental group of rats is trained to find a submerged platform, with a landmark attached to it, located in one corner of a rectangular pool: the correct corner (see figure 6.01).

According to Miller and Shettleworth (2007) each location of the pool (L) comprises several elements (E) corresponding to the CSs of classical conditioning experiments. Four elements, B, F, G, and W can be used to describe the apparatus depicted in the figure. Element B represents one out of several possible cues that exist at every corner, such as particular pattern of light and shade or corner-angle. Due to the arena's axial symmetry the correct (Corr) and geometrically equivalent corners (Rot) have the same geometric properties, defined as element G. The incorrect corners of the pool (Near and Far) also have the same geometric properties but are the mirror image of other two, and are represented by element W. Finally, F denotes the landmark. Thus, element B is present at every corner, element F at only the correct corner; G at the correct and geometrically equivalent corners and W is present at the Near and Far corners of pool. P gives the location of the submerged platform, attached to which is the landmark, or feature (F). The letters, B, F, G and W denote elements in the model proposed by Miller and Shettleworth (2007). Corr signifies the correct corner and Rot the geometrically equivalent corner. The incorrect corners have been labelled Near and Far.

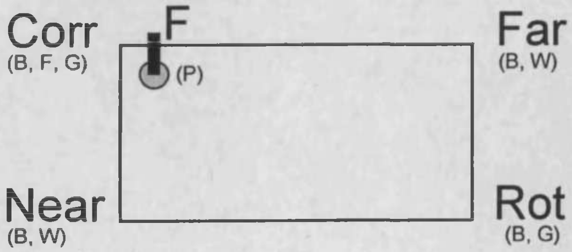

Figure 6.01. The rectangular swimming pool used to describe a hypothetical experiment.

Miller and Shettleworth's theory (2007) is described by the equations below:

a.

$$\Delta V_E = \alpha .\ \beta\ (\lambda - \Sigma V_L)\ P_L$$

P_L is different for every corner:

b.

$$P_{Corr} = V_F + V_B + V_G / V_{Corr} + V_{Rot} + V_{Near} + V_{Far}$$

$$P_{Rot} = V_B + V_G / V_{Corr} + V_{Rot} + V_{Near} + V_{Far}$$

$$P_{Near} = V_B + V_W / V_{Corr} + V_{Rot} + V_{Near} + V_{Far}$$

$$P_{Far} = V_B + V_W / V_{Corr} + V_{Rot} + V_{Near} + V_{Far}$$

As with the Rescorla-Wagner model (1972), the parameters α and β capture the salience of the CS and US respectively. Miller and Shettleworth (2007) initially set the latter value at 1 and the former, being the same for every element, at 0.15; so that the product of α. β is always 0.15. The first term in equation a. describes, for each trial, the change in associative strength of an element (ΔV_E) as a function of the difference between the maximum associative strength the US (λ) can support and the sum of the associative strengths of the elements present at the same location (ΣV_L). Put more simply elements present at the same location will compete directly for the control they acquire over behaviour, in much the same way as that predicted by the Rescorla-Wagner model (1972). The change in associative strength of the landmark (ΔV_F), for instance, is given by: $(\lambda - V_B + V_F + V_G)$. Learning based on the landmark is thus influenced by the degree of learning based on every element, B, F and G, present at the correct location (Corr).

When locations are rewarded, λ has a value of 1 but has a value of 0 when they are unrewarded. Consequently elements present only at the correct location (Corr) will gain associative strength whilst those present at the remaining incorrect locations will lose it. In the example, if subjects should swim towards the correct corner (Corr) and escape onto the platform, the associative strength of elements B, F and G, are predicted to increase. At the same time elements G and B will also lose associative strength, due to the absence of the platform in the geometrically equivalent corner (Rot). Similarly, the Near and Far corners never contain the platform and swimming towards them will result in elements B and W losing associative strength. In fact, according to Miller and Shettleworth (2007) element W should gain negative associative strength and become a conditioned inhibitor, a prediction that might be worthy of investigation in the future.

Some elements appear at more than one location. In these circumstances the net change in associative strength is given by summing the ΔV_E at every location occupied by E. Thus, the net change in associative strength of element G, on each trial, is given by summing what was learned about this element at the correct and geometrically equivalent corners $[\Delta V_G = \alpha.\ \beta\ (1 - V_B + V_F + V_G) + \alpha.\ \beta\ (0 - V_B + V_G)]$.

The final term of equation a., and given for each corner in b., describes the probability of subjects choosing a particular location (P_L) on any given trial. At the outset of training all choices are assumed to be are equally probable ($P_{Corr} = P_{Rot} = P_{Near} = P_{Far}$). In the rectangular pool the probability of rats swimming towards the correct corner at the start of training is thus 0.25, or 25%. However P_L is influenced by the degree of learning about all the elements present at a particular location (V_L), relative to the total associative strengths of the elements present at every other location (ΣV_L). As a result the probability of choosing the correct corner [$P_{corr} = (V_{B+} V_F + V_G) / (V_{corr} + V_{rot} + V_{near} + V_{far})$], will increase as training progresses whilst the reverse happens to the near and far corners. The probability of choosing the geometrically equivalent corner will also increase, but to a lesser extent than the correct corner, due to the absence of the landmark [$P_{rot} = (V_{B+} + V_G) / (V_{Corr} + V_{Rot} + V_{Near} + V_{Far})$].

Multiplying the first by second term in the equation above is central to understanding why a landmark can sometimes potentiate learning based on the geometry of an environment and can lead to what Miller and Shettleworth (2007) have called feature enhancement. As already noted, escaping onto the platform will result in element G gaining associative strength at the correct corner, but losing it at the geometrically equivalent corner. However, the landmark will acquire control over the behaviour of rats more quickly than the correct geometry of the pool because it unambiguously describes the location of the platform. The presence of the landmark will therefore increase the probability of rats swimming to the geometrically correct corner which in turn will increase the associative strengths of all the elements present at that location, including element G. As a result G will gain more associative strength at the correct corner than it loses at the geometrically equivalent corner and learning based on geometry of the pool will proceed more quickly than if rats had been trained without the landmark. The presence of the landmark will therefore initially enhance rather than restrict learning based on the geometry of the pool.

Miller and Shettleworth (2007) have also argued that the process of feature enhancement can offer one way to explain the failures of a landmark to block learning based upon shape of an environment (Hayward et al 2003; 2004; Wall et al 2004). To illustrate this process it shall be assumed that the experimental group in the example was trained first to find the platform with a landmark attached to it, before being trained in the rectangular pool with the same landmark attached to the platform. Assuming that there were no other cues in the pool during the pre-training stage then prior training will have ensured that the landmark acquired considerable control over searching for the platform. At the outset of the second stage the associative strength of the landmark will already be high which will increase the probability of rats swimming to the correct corner. As a result, rats will be more likely to swim to the correct corner of the pool, at least over the initial trials of the Stage 2 training, and learn more about the geometry of the pool than a control group which did not receive prior training with the landmark.

The authors admit, that feature enhancement is a transitory process which occurs when the associative strengths of the elements are relatively small (Miller & Shettleworth, 2007). When the control acquired by the feature is sufficiently large it will restrict that acquired by the shape of the pool. Thus, potentiation, overshadowing and even blocking of geometric learning by a landmark is predicted to be dependent upon the number of trials animals receive and at which point during conditioning they are tested. Early testing with few trials, should result in potentiation, whilst late testing with many trials should result in cue competition. Unfortunately, such ideas seem to be inconsistent with the available empirical evidence Experiments conducted by Pearce and his colleagues (Pearce et al, 2001; 2006; Graham et al, 2006) found evidence of potentiation even though animals received extensive training, before being tested. Similarly, Experiment 6 revealed a potentiation effect despite animals being tested after a lengthy period of training (see, Hayward et al 2003). It is perhaps also worth noting that in their own simulations Miller and Shettleworth (2007) observed the effects of feature enhancement for as few as four trials: by the fifth trial this phenomenon had disappeared. Given the fragility of feature enhancement, it is difficult to understand just how this process could explain the robust absences of overshadowing and potentiation observed in my own studies and elsewhere (Pearce et al, 2001; 2006; Hayward et al 2003; Graham et al, 2006).

The theory proposed by Miller and Shettleworth (2007), in its simplest form, can thus offer one way to explain the many failures of landmark to restrict spatial learning based on the shape of environment that can be found in this thesis. The theory, however, makes many assumptions which may or may not be correct. Miller and Shettleworth (2007) include in their model, element (B), present at every corner, which they assume to have an associative strength of 0.1 before the start of conditioning. Unfortunately, there is no empirical justification for B having this value and the remaining elements in the model would gain never gain associative strength if it is assumed that B has value of Zero instead. Changing the learning rate parameters, such as the saliency of the landmark (α), can also have a serious impact on the behaviour of the model and without a method of independently assessing stimulus salience it is difficult to understand how this problem might be overcome. The model proposed by Miller and Shettleworth (2007) does, however, offer a new way to interpret the failures of a landmark to restrict spatial learning based on the shape of an environment (Cheng; 1986: Kelly et al, 1998; Pearce et al, 2001) and it can be used to make predictions which should provide some impetus for future research.

In the final experiment an attempt was made to assess if navigation was based on a local cue or on the overall shape of the environment as Cheng (1986) and Gallistel (1990) argue. The ability of rats to find the submerged platform in the rectangular array transferred to the kite-shaped array. It is therefore unlikely that rats referred to the overall shape of the original apparatus to find the platform, which undermines the idea that animals possess a Geometric Module (Cheng; Gallistel). Rats must have therefore had some other strategy at hand for escaping from the pool, several of which were discussed in the previous chapter. One possibility is that rats developed a habit of turning in a particular direction upon being released into the pool and the tendency rats exhibited for searching the apex and opposite corners of the kite tends to support this point of view. Such ideas are not only consistent with other research (Esber et al, 2005; Pearce et al, 2004) but they also suggest that behaviour which appears to be under the control of an array of landmarks might instead be under the control of local cues. If there is any generality to these ideas then it might also be necessary to offer a similar explanation for behaviour which appears to under the control of an environment with enclosed walls. It is perhaps worth noting that Pearce et al (2004) have trained rats to find a submerged platform situated in one corner of a rectangular pool with enclosed walls and found evidence to suggest that rats habitually turned in a particular direction upon being released, which enabled subjects to escape from the pool. Whether rats used similar habits to find the platform in my own experiments is unclear, but it certainly cannot be ruled out.

None of my experiments have provided any indication to suggest that the presence of a featural cue like a landmark or the presence of room cues restricted learning based on the shape of the pool. Such results are consistent with the ideas expressed in the theory of the Geometric Module (Cheng, 1986; Gallistel, 1990). However, evidence of potentiation and the suggestion that navigation may be based on local rather than global cues is difficult to explain in terms of animals having a Geometric Module (Cheng, 1986; Gallistel, 1990). By comparison the associative model of geometric learning proposed by Miller and Shettleworth (2007) can explain why landmark can sometimes restrict; whilst at other times potentiate learning based on the shape of an environment. Even so, it may be more appropriate to interpret behaviour which appears to be under the control of the shape of an environment in terms animals acquiring habits based on local rather than global cues. Of course the problem is now raised of identifying the circumstances in which the acquisition of such habits will prevent blocking and overshadowing from being observed.

Before closing the discussion, it is perhaps necessary to offer a parsimonious account of all the data presented throughout this thesis. All attempts to reveal the effects of cue competition between cues placed inside and outside the shape of an environment failed. One way to explain such failures is to argue that the effects of cue competition were masked by the effects potentiation, but the outcome of Experiment 8 makes this account unlikely. Another possibility is that rats may have directed so much of their attention to the shape of the environment that they failed to attend to other relevant cues placed inside or outside the pool. If this analysis is correct then there is no reason to suspect that cue competition should have succeeded (see Mackintosh, 1973). Such ideas deserve little merit, however, because they are incompatible with the current data. When a landmark was situated in the same corner of the pool as the platform, or when room cues surrounded the pool (and remained in the same orientation as it) rats escaped onto the platform more quickly than when these additional cues were absent. Rats must have therefore paid at least some attention to these additional cues.

Upon being released into the pool rats had no alternative but to swim. Often, at the outset of training the author observed rats holding onto the base of the landmark and climbing on top of it, a tendency which rats found difficult to relinquish. Rats may have therefore headed directly towards the landmark as a means of escaping from the pool. Such behaviour may have been guided by a stereotypical stimulus-response association and the landmark, at least at the beginning of training, would be expected to gain little associative strength. Over the course of training rats eventually gave up this strategy for escaping from the pool. However, the initial trials may have prevented the landmark from acquiring sufficient associative strength to restrict spatial learning based upon the shape of the pool. It is difficult to see how this analysis could be used to explain the failure of room cues to restrict learning based on the shape of environment.

One obvious and simple way to explain the failures to observe cue competition, which has been alluded to on many occasions, is to appeal to the acquisition of habits. The results of the final experiment implied that rats found the platform by turning in a particular direction upon being released into the pool. In addition is was argued that the potentiation observed in Experiment 6 could be explained sufficiently well by assuming that Group Stable acquired a greater habit of swimming in the correct area of pool than the relevant control groups. It may be somewhat of a leap to explain the results of all my experiments in terms of release-habits or habits for swimming in particular area of the pool but this possibility cannot be ruled out. The acquisition of habits may therefore offer a more parsimonious account for the failures to observe cue competition described here, than alluding to the ideas expressed in the Geometric Module (Cheng, 1984; Gallistel, 1990).

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