

An associative analysis of spatial learning in environments with a distinctive shape

Murray R. Horne

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Thesis Summary

The aim of this thesis was to evaluate the proposal by Miller and Shettleworth (2007) that learning about geometric cues in environments with a distinctive shape is governed by a competitive learning rule (e.g., Rescorla & Wagner, 1972). To do this, in all experiments, rats were trained to locate a hidden platform by reference to the shape of a swimming pool.

Chapter 2 (Experiments 1-4) assessed whether a landmark suspended above the platform would overshadow learning about geometric cues. No overshadowing was recorded, even when the salience of the geometric cues was reduced. These findings are inconsistent with the model of Miller and Shettleworth (2007).

In Chapter 3 (Experiments 5-7), a blocking paradigm was used. When rats were given extended pre-training with a landmark above the platform, only then did the landmark successfully block learning about geometric cues. However, some unexpected findings suggested that perhaps the spatial cues were competing for attention rather than associative strength.

The experiments in Chapter 4 (Experiments 8 and 9) successfully demonstrated superconditioning of geometric cues by an inhibitory landmark providing convincing evidence that learning about geometric cues is governed by the principles of associative learning. Miller and Shettleworth's (2007) model however, failed to predict this outcome.

Experiments 10-13 in Chapters 5 and 6 showed that associations formed between geometric and non-geometric cues. This outcome provides the basis for a viable explanation for potentiation and for the past failures to find cue competition in the spatial domain.

The empirical findings of this thesis show that learning about geometric cues is not entirely void of associative processes as once thought. A number of recent models of spatial learning are discussed.

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I would like to thank John Pearce for his continued guidance and support throughout this project. His commitment to research and teaching is truly remarkable and inspiring. As a young researcher at the beginning my career, I am grateful to have this opportunity to work with him and I can honestly say that he is an academic role model that all young researchers should aspire to become.

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Table of Contents

Declaration.....	ii
Thesis Summary.....	iii
Acknowledgments.....	iv
Table of Contents.....	v
List of Tables	ix
List of Figures	x
Chapter 1: General Introduction	1
1.1. Cue Competition: The Rescorla-Wagner (1972) Model.....	1
1.1.1. Overshadowing and the Rescorla-Wagner Model	2
1.1.2. Blocking and the Rescorla-Wagner Model.....	3
1.2. Is Spatial Learning Special? I. Cognitive Map Considerations	3
1.2.1. Overshadowing in the Spatial Domain	5
1.2.2. Blocking in the Spatial Domain.....	10
1.2.3. Landmark Stability.....	12
1.2.4. Is There a Need for a Cognitive Map?.....	17
1.3. Is Spatial Learning Special: II. Geometric Module Considerations	20
1.3.1. The Geometric Module.....	21
1.3.2. Early Support for the Geometric Module	23
1.3.3. Further Support for the Geometric Module – Cue Competition Studies	24
1.4. Potentiation, Overshadowing, and Blocking In Environments with a Distinctive Shape	28
1.5. An Associative Model of Geometry Learning (Miller & Shettleworth, 2007).....	33
1.5.1. Failure to Find Overshadowing of Geometric Cues-Miller & Shettleworth (2007)	36

1.5.2. Failure to Find Blocking of Geometric Cues-Miller & Shettleworth (2007)	39
1.5.4. Limitations of Miller and Shettleworth's (2007) Model.....	42
1.6. Organisation and Rationale for Thesis.....	44
Chapter 2: The effect of geometric salience on overshadowing in an environment with a distinctive shape.....	45
2.1. Introduction.....	45
2.2. Experiment 1	47
2.2.1. Method	49
2.2.2. Results and Discussion	52
2.3. Experiment 2.....	56
2.3.1. Method	59
2.3.2. Result and Discussion	60
2.4. Experiment 3	63
2.4.1. Method	64
2.4.2. Results and Discussion	65
2.5. Experiment 4.....	68
2.5.1. Method	68
2.5.2. Results and Discussion	69
2.6. Summary and Conclusions	72
Chapter 3: A landmark blocks searching for a hidden platform in an environment with a distinctive shape after extended pre-training.....	74
3.1. Introduction.....	74
3.2. Experiment 5.....	76
3.2.1. Method	77
3.2.2. Results and Discussion	79

3.3. Experiment 6.....	83
3.3.1. Method.....	83
3.3.2. Results and Discussion.....	83
3.4. Experiment 7.....	88
3.4.1. Method.....	89
3.4.2. Results and Discussion.....	90
3.5. Summary and Conclusions.....	97
Chapter 4: Conditioned inhibition and superconditioning in an environment with a distinctive shape.....	102
4.1. Introduction.....	102
4.2. Experiment 8.....	103
4.2.1. Method.....	106
4.2.2. Results and Discussion.....	108
4.3. Experiments 9a and 9b.....	115
4.3.1. Method.....	118
4.3.2. Results and Discussion.....	120
4.4. Summary and Conclusions.....	129
Chapter 5: Between-cue associations influence searching for a hidden goal in an environment with a distinctive shape.....	140
5.1. Introduction.....	140
5.2. Experiment 10.....	143
5.2.1. Method.....	146
5.2.2. Results and Discussion.....	147
5.3. Experiment 11.....	152
5.3.1. Method.....	153

5.3.2. Results and Discussion	154
5.4. Summary and Conclusions	160
Chapter 6: Between-cue associations form between a landmark and geometric cues in an environment with a distinctive shape.....	162
6.1. Introduction.....	162
6.2. Experiment 12.....	164
6.2.1. Method	165
6.2.2. Results and Discussion	168
6.3. Experiment 13	175
6.3.1. Method	177
6.3.2. Results and Discussion	179
6.4. Summary and Conclusions	184
Chapter 7: General Discussion.....	188
7.1. Implications of Between-Cue Associations	191
7.2. Implications of Findings for Potentiation in the Spatial Domain	193
7.3. Implications of Findings for Cheng and Newcombe's (2005) Modular Theories.....	196
7.4. Implications of Findings for Spatial Learning Based on Surface Boundaries.....	197
7.5. Implications of Findings for View-Based Matching Accounts of Spatial Learning ..	199
7.6. Final Remarks and Future Directions	201
References.....	206

List of Tables

Table 6.1. <i>Design of Experiment 13 showing training environments and the landmarks that were present during each stage of the experiment.....</i>	176
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List of Figures

<i>Figure 1.1.</i> Schematic representation of the training conditions for the shape + colour and shape only groups in the experiment by Graham et al. (2006).	29
<i>Figure 1.2.</i> Schematic representation of the training conditions for the three groups in the experiment by Pearce et al. (2006).	31
<i>Figure 1.3.</i> A schematic representation of typical overshadowing, blocking and potentiation designs in a swimming pool with the elemental components that Miller and Shettleworth (2007) suggest form each environment.....	34
<i>Figure 1.4.</i> The results from computer simulations of the overshadowing experiment shown in the first row of Figure 1.1 based on the associative model of geometry learning by Miller and Shettleworth (2007).....	38
<i>Figure 1.5.</i> The results from computer simulations of the blocking experiment shown in the second and third row of Figure 1.1 based on the associative model of geometry learning by Miller and Shettleworth (2007).....	41
<i>Figure 2.1.</i> Schematic representation of the training conditions for the overshadowing and two-landmark control groups in Experiment 4 of Pearce et al. (2001).....	46
<i>Figure 2.2.</i> The results from computer simulations of an overshadowing experiment with an overshadowing and two-landmark control group based on the associative model of geometry learning by Miller and Shettleworth (2007).....	48

<i>Figure 2.3.</i> Mean escape latencies and mean percentage of correct choices for the overshadowing and control groups of Experiment 1.	53
<i>Figure 2.4.</i> Mean (+SEM) percentage of time spent in the correct and incorrect zones during the geometric test trials on Session 12 and on Session 24.	55
<i>Figure 2.5.</i> The results from computer simulations based on the associative model of geometry learning by Miller and Shettleworth (2007). For one simulation the salience of the landmark was reduced to 0.01 and for the other simulation the salience of the geometric cues were reduced to 0.01.....	57
<i>Figure 2.6.</i> Mean time to find the submerged hidden platform for the high and low salience groups of Experiment 2.....	61
<i>Figure 2.7.</i> Mean percentage of time spent in the correct zone on multiple test trials conducted for the high and low salience groups of Experiment 2.....	62
<i>Figure 2.8.</i> Mean escape latencies and mean percentage of correct choices for the overshadowing and control groups of Experiment 3.	66
<i>Figure 2.9.</i> Mean (+SEM) percentage of time spent in the correct and incorrect zones for the overshadowing and control groups during the geometry test trials of Experiment 3.	67

<i>Figure 2.10.</i> Mean escape latencies and mean percentage of correct choices for the overshadowing and control groups of Experiment 4.	70
<i>Figure 2.11.</i> Mean (+SEM) percentage of time spent in the correct and incorrect zones during geometry test trial for the overshadowing and control groups of Experiment 4.	71
<i>Figure 3.1.</i> Mean percentage of correct choices across Stage 1 and Stage 2 for the blocking, control-1 and control-2 groups of Experiment 5.....	80
<i>Figure 3.2.</i> Mean (+SEM) percentage of time spent in the correct and incorrect zones during the geometry test for the blocking, control-1 and control-2 groups of Experiment 5.	82
<i>Figure 3.3.</i> Mean percentage of correct choices across Stage-1 and Stage-2 training for the blocking and control groups of Experiment 6.....	85
<i>Figure 3.4.</i> Mean (+SEM) percentage of time spent in the correct and incorrect zones for the blocking and control groups during a geometry test trial of Experiment 6.	86
<i>Figure 3.5.</i> Mean escape latencies to find the hidden platform across Stage-1 training and the mean percentage of correct choices made across Stage-2 training for the blocking and control groups of Experiment 7.....	92
<i>Figure 3.6.</i> Mean (+SEM) percentage of time spent in the correct and incorrect zones during a geometry test trial and the mean (+SEM) percentage of time spent in the correct zone during the landmark test for the four groups of Experiment 7.	94

<i>Figure 3.7.</i> The mean percentage of time spent in the correct zone for the four extinction trials of the landmark for the blocking-24 and blocking-12 groups of Experiment 7.	95
<i>Figure 4.1.</i> Schematic representation of the training stages of Experiment 8.	104
<i>Figure 4.2.</i> Mean percentage of correct choices on A+ trials across Stage 1 and on A+ and AX- trials across Stage 2 of Experiment 8.	109
<i>Figure 4.3.</i> Mean percentage of correct choices on B+ trials across training in Stage 3 and the mean (+SEM) percentage of time spent in the correct and incorrect zones during the B- and BX- test trials (summation test) of Experiment 8.	111
<i>Figure 4.4.</i> Mean percentage of correct choices across Stage-4 training (retardation test) for Group X+ and Group Y+ of Experiment 8.	113
<i>Figure 4.5.</i> Schematic representation of the training stages of Experiments 9a and 9b.	117
<i>Figure 4.6.</i> Mean percentage of correct choices across Stage-1 training for the superconditioning and control groups of Experiments 9a and 9b.	121
<i>Figure 4.7.</i> Mean percentage of correct choices on A+ and AX- trials across training in Stage 2 for the superconditioning and control groups of Experiments 9a and 9b.	122

<i>Figure 4.8.</i> Mean (+SEM) percentage of time spent in the correct zone during the A- and AX- test trials for the superconditioning and control groups of Experiments 9a and 9b.	124
<i>Figure 4.9.</i> Mean percentage of correct choices for the superconditioning and control groups across Stage-3 training of Experiments 9a and 9b.....	125
<i>Figure 4.10.</i> Mean (+SEM) percentage of time spent in the correct zone during the A- test trial conducted before and after Stage-3 training for the superconditioning and control groups of Experiments 9a and 9b.	127
<i>Figure 4.11.</i> Simulated training data based on Miller and Shettleworth's (2007) model of learning about geometric cues for Experiment 9a.	133
<i>Figure 4.12.</i> Simulated results of Experiment 9a based on Miller and Shettleworth's (2007) model of learning about geometric cues..	134
<i>Figure 4.13.</i> The accumulation of associative strengths for each cue of Experiment 9a based on the associative model of geometry learning by Miller and Shettleworth (2007).....	135
<i>Figure 5.1.</i> A plan of the apparatus used for the two groups in the three stages of Experiment 10.....	144
<i>Figure 5.2.</i> The mean percentages of correct choices made during each session of training in the kite and revaluation training in the square for the Consistent and Inconsistent groups of Experiment 10.....	148

<i>Figure 5.3.</i> The mean (+SEM) percentages of time spent in the correct and incorrect quadrants during the test trial of Experiment 10.....	150
<i>Figure 5.4.</i> The mean percentages of correct choices made during each session of training in the kite and revaluation training in the square for the Consistent and Inconsistent groups of Experiment 11.....	155
<i>Figure 5.5.</i> The mean (+SEM) percentages of time spent in the correct and incorrect zones during Test 1 and Test 2 of Experiment 11.....	157
<i>Figure 6.1.</i> Mean percentage of correct choices during Stage 1 for the overshadowing and control groups of Experiment 12.	169
<i>Figure 6.2.</i> The mean (+SEM) percentage of time spent in the correct and incorrect zones during a 60-s geometry test in Session 14 and the mean (+SEM) percentage of time spent in the correct and incorrect zones during the first 15 s of the same geometry test of Experiment 12.....	170
<i>Figure 6.3.</i> Mean percentage of correct choices across Stage 2 for the consistent and inconsistent groups of Experiment 12.....	171
<i>Figure 6.4.</i> The mean (+SEM) percentage of time spent in the correct and incorrect zones during a 60-s geometry test in the triangle following Stage 2 and the mean (+SEM)	

percentage of time spent in the correct and incorrect zones during the first 15 s of the same geometry test for Experiment 12..... 173

Figure 6.5. The mean percentage of correct choices across Stage-1 training in the triangle and rectangular environments of Experiment 13..... 180

Figure 6.6. The mean percentage of correct choices across Stage 2 and the percentage of time spent in correct zone during non-reinforced trials during Stage 2 in the triangle consistent and rectangle consistent groups of Experiment 13..... 181

Figure 6.7. The mean (+SEM) percentage of time spent in the correct and incorrect zones during a geometry test in the triangle and rectangle following Stage-2 training for the triangle consistent and rectangle consistent groups of Experiment 13. 183

Chapter 1: General Introduction

The success of associative theories of learning (e.g., Rescorla and Wagner, 1972) spans across species from bees (e.g., Bitterman, Menzel, Fietz, & Schäfer, 1983) to humans (Larkin, Aitkin, & Dickinson, 1998). The theories have also had great success explaining a wide range of phenomena from blocking and overshadowing (Kamin, 1969a; Pavlov, 1927) to causal learning (e.g., Larkin et al., 1998). The question that is at the basis of this thesis is to what extent can associative learning principles be applied to spatial learning, that is, how are cues that are located some distance from the animal used to locate specific goals within its immediate environment? One way to address this question is to see if overshadowing and blocking can be observed in spatial tasks. These two phenomena have been taken as evidence that the principles of associative theories of learning apply in the conditioning chambers and thus provide an excellent framework from which to start.

Overshadowing and blocking epitomise the principle of cue competition which is the idea that cues interact with each other and compete for the control they acquire over a specific behaviour. This principle is fundamental to most associative theories of learning. One such theory, and perhaps the most influential of all the associative theories, is the Rescorla-Wagner (1972) model. By way of background I shall start by describing the model and then how it explains overshadowing and blocking.

1.1. Cue Competition: The Rescorla-Wagner (1972) Model

The main principle of the Rescorla-Wagner (1972) model is that stimuli or cues in the animals' immediate environment (i.e., the conditioning chamber or an enclosed spatial arena) compete with each other for control they acquire over a specific behaviour. The Rescorla-Wagner model assumes an animal learns that a conditioned stimulus (CS) predicts an unconditioned stimulus (US) over the course of training through an error-correction process.

In other words, an animal computes an error term based on the difference between what is expected to occur on a given trial and what actually happens. The error term is assumed to influence the growth of an association between the CS and US, and the stronger this association the greater will be the strength of the conditioned response (CR) elicited by the CS. The mathematical derivation of the model is given in Equation 1.1, where ΔV is the change in the associative strength of a CS on a given trial, α is the inherent salience of that CS, β and λ , are respectively, a learning rate parameter and asymptotic value pertaining to the US, and $\sum V$ is the sum of the associative strengths of all the CSs present during the given trial.

$$\Delta V = \alpha\beta(\lambda - \sum V) \quad (\text{Equation 1.1})$$

Three principles follow from Equation 1.1. First, the change of the associative strength of one CS is inversely proportional to the existing associative strength of that CS and the sum of the associative strength of all other CSs concurrently present during a given trial ($\sum V$). Second, the magnitude of the changes in associative strength across trials decreases in an incremental fashion so that the difference between the asymptotic value of the US, which is finite, and the sum of the associative strengths of the CSs present on a given trial ($\lambda - \sum V$) is larger early in training when the associative strengths of the CSs are relatively low, than late in training, when the associative strengths of the CSs are relatively high. Finally, the magnitude of the change in associative strength is directly proportional to the salience of the CS (α) and the US (β), which are both held constant for the course of training.

1.1.1. Overshadowing and the Rescorla-Wagner Model

In a typical overshadowing design, two stimuli (A and B) are paired together followed by reinforcement. According to the Rescorla-Wagner (1972) model, A and B both acquire

associative strength at the same rate, however, there is only a finite amount of associative strength, thus each cue can only gain a maximum of 50% of the given associative strength (under the assumption that A and B are of equal salience). For a scenario where only one stimulus is conditioned, then all the associative strength can be acquired by the single cue. Therefore in the above scenario, the presence of B is said to overshadow learning about A and conversely, the presence of A restricts learning about B.

1.1.2. Blocking and the Rescorla-Wagner Model

Kamin (1969a; 1969b) described a phenomenon in which during one stage of training, a stimulus, A, was followed by reinforcement. In a subsequent stage, A was paired with a novel stimulus, B, and was again followed by reinforcement. Tests with B resulted in less conditioned responding, compared to a control group that did not receive the first stage of training, hence, learning about A in the experimental group restricted or blocked learning about B.

The Rescorla-Wagner (1972) model explains blocking in the following way. During the first stage of training, A would gain some amount of associative strength, so that during the second stage of training, the novel stimulus, B, would have the opportunity to gain only a modest level of associative strength because the majority of associative strength was taken up by A during the first stage.

1.2. Is Spatial Learning Special? I. Cognitive Map Considerations

Some researchers have argued that associative principles do not govern certain aspects of spatial learning and as such a competitive rule that embodies the Rescorla-Wagner (1972) model does not apply to all aspects of spatial learning. This idea goes against the claim that associative learning principles are general and apply to a wide range of tasks

(Bitterman, 2000). Particularly forceful advocates of this idea are O'Keefe and Nadel (1978). O'Keefe and Nadel postulated two navigational systems, a taxon and a locale system. On one hand, the taxon system encompasses simple cue learning. Learning to find a goal with respect to an intra-maze cue such as a local landmark or beacon would be considered part of the taxon system. Learning in this system is thought to progress incrementally by the acquisition of multiple stimulus-response associations and is thus in keeping with the principles of associative learning theories. On the other hand, the locale system is controlled by map-like representations of the environment. Animals are assumed to use the relationship among cues in their environment to identify their current position on the map and to locate specific goals with reference to the map. An evaluation of the locale system will be the focus of this section as it is learning within this system that O'Keefe and Nadel regard as being unaffected by principles such as those embodied in the Rescorla-Wagner (1972) rule.

First, O'Keefe and Nadel (1978), suggested that when an "animal first enters a novel situation all the misplace detectors will be activated and exploration will continue until sufficient information is incorporated into the map of that environment" (p. 94) and as a result of this process, "whenever an organism attends to an object it is encoded in the map" (p. 95). This suggestion implies that the cognitive map is continuously updated and previous experience with spatial cues should have no influence on whether a novel cue is incorporated into the map, as long as the new cue is attended to. These statements are in contrast to associative learning principles that predict cue competition such as overshadowing and blocking. Second, O'Keefe and Nadel suggested that the "incorporation of information about stimuli occurs in a non-incremental fashion" (p. 95), which is in contrast to associative learning theories that predict learning across trials is incremental (e.g., Rescorla and Wagner, 1972). Finally, O'Keefe and Nadel further remark that "the mapping system is sensitive to constant variability in the environment; such variability makes it difficult, if not impossible,

to build a useful map” (p. 95). This last statement is hard to interpret and construct a testable hypothesis from, but researchers (e.g., Beigler and Morris, 1993; 1996) have taken it to suggest that any cue that is perceived as being unstable with respect to a stable global frame of reference will not be used as a landmark and as such would not be incorporated into a map. Associative theories have no problem with animals learning the significance of an unstable landmark as long as the landmark maintains its position relative to a goal, but importantly, the landmark does not have to be stable with respect to a stable global framework.

If associative principles govern spatial learning, then these three claims proposed by O’Keefe and Nadel (1978) are in contrast to those that follow from associative principles. The following sections will evaluate the three claims of O’Keefe and Nadel with respect to overshadowing, blocking and landmark stability in spatial learning.

1.2.1. Overshadowing in the Spatial Domain

As we have seen in overshadowing in Pavlovian conditioning, when two cues are presented together, each cue restricts learning about the other cue. That is, the control acquired by each cue when two cues are conditioned together is less than if only a single cue is conditioned. According to O’Keefe and Nadel (1978) the number of cues present during training would not influence the amount of control each cue has gained because the formation of a cognitive map is said to occur in an all-or-none fashion. In this case, all cues should gain the same amount of control over the animals’ behaviour. Showing evidence that overshadowing occurs in the spatial domain would strongly go against the claim that learning in spatial domain occurs in an all-or-none fashion.

Chamizo, Sterio, and Mackintosh (1985) were the first to look at overshadowing between spatial cues. They trained rats on a Y-maze that had distinct intra-maze cues on each of the goal arms. One of the two goal arms was covered in sandpaper and the other goal

arm was covered in black rubber. One group of rats was trained with intra-maze cues relevant, another group with extra-maze cues relevant and the experimental group was trained with both extra-maze and intra-maze cues relevant. When tested in the presence of intra-maze cues alone, rats in the group trained with both intra- and extra-maze cues relevant showed impaired performance compared to the group trained with just intra-maze cues. Clearly, extra-maze cues overshadowed learning about the significance of intra-maze cues. There was, however no evidence of reciprocal overshadowing of extra-maze cues by intra-maze cues. In a later report, March, Chamizo, & Mackintosh (1992), suggested that in the previous study, the group trained with just extra-maze cues relevant made more errors during training compared to the group that was trained with both extra-maze and intra-maze cues relevant and thus had less opportunity to learn about extra-maze cues. However, using the same experimental apparatus, when each group was equated on the number of reinforced and non-reinforced trials, and thus had equal opportunity to learn about the extra-maze cues, they replicated their previous finding and also showed that learning about intra-maze cues now overshadowed extra-maze cues.

A similar result was obtained in a swimming pool by Redhead, Roberts, Good, and Pearce (1997). Rats were trained to search for a submerged platform that was either located with respect to only distal cues located on the walls of the experimental room or by both distal cues and a beacon attached to the platform. Both groups were then tested in the absence of the beacon and platform. The group that received training in the presence of the beacon spent significantly less time in the vicinity of the pool where the platform had been previously located during training compared to the group that had to rely solely on distal cues to navigate. The beacon overshadowed learning about distal cues.

The aforementioned studies (Chamizo et al., 1985; March et al., 1992; Redhead et al., 1997) all suggest that extra-maze cues and intra-maze cues interact with each other and

compete for the control over spatial behaviour in ways that are consistent with the principles of associative learning. It is clear that learning to locate a goal with reference to extra-maze or intra-maze cues does not occur in an all-or-none fashion, consistent with the principle of cue competition. The following studies that look at overshadowing between distal landmarks strengthen support for this conclusion.

Sanchez-Moreno, Rodrigo, Chamizo and Mackintosh (1999) showed that redundant distal landmarks, located within a curtain that encircled the pool, are susceptible to overshadowing. They trained a control group in a swimming pool to locate a hidden platform with reference to an array of distal landmarks, ABCD, with the distance between each landmark and its neighbour being constant. The overshadowing group was trained with ABCD+X, where X was an auditory cue that shared the same spatial location as landmark D. When the two groups were tested with the landmark configuration, ACD, in the absence of the platform, the overshadowing group spent less time in the vicinity of the pool where the platform was located during training compared to the control group. It was later shown in a different experiment that when both groups were tested with the landmark configuration ACX, the overshadowing group again spent less time in the vicinity of the pool where the platform was located during training compared to the control group that received training with the landmark array, ABCX. These results provided evidence of reciprocal overshadowing between landmark D and the auditory cue X. (Sanchez-Moreno et al., 1999, Experiment 2). Second, Goodyear and Kamil (2004) found that relative proximity of the landmark to the goal was a key attribute that determined if a landmark was overshadowed or not. They trained Clark's nutcrackers to locate a goal with respect to an array of different landmarks, where each landmark was located at a specified distance from the goal. In a close group, four landmarks were located 30 cm, 50 cm, 70 cm, and 90 cm from the goal. In a medium group, the four landmarks were located 50 cm, 70 cm, 90 cm, and 110 cm from the

goal and finally in a far group the four landmarks were located 70 cm, 90 cm, 110 cm, and 130 cm from the goal. In all groups, the landmark that was located closest to the goal acquired more control over spatial search for the food than the remaining landmarks during single landmark tests in the absence of any reinforcement. Thus the landmark that was 50 cm from the goal gained more control in the medium group than in the close group. This result suggested that closer landmarks overshadowed learning the location of the goal with reference to more distal landmarks. For a similar example in pigeons using a touch-screen task see Spetch (1995)

These two studies (Sanchez-Moreno et al., 1999; Goodyear and Kamil, 2004) clearly show that spatial learning follows associative principles. On the one hand, according to O'Keefe and Nadel (1978), in the study by Sanchez-Moreno et al. (1999), cues ABCD plus the auditory cue X would be incorporated into the map. O'Keefe and Nadel suggested that if animals are using a map, then "any cue, or group of cues, can be removed from the total array without preventing the remainder (so as long as at least two or three remain) from uniquely specifying, by their relation, a particular place" (p. 93). Thus it follows that during testing of ACD or ACX, the presence of three cues should be enough to maintain use of the map, so during testing, performance should have been equivalent in both the control and overshadowing groups. On the other hand, if learning about spatial cues follows the principles of associative learning, then cues D and X would compete for associative strength in the overshadowing group and thus learning about either cue would be restricted due to the presence of the other cue. From this account, it then follows that during a test trial with ACD or ACX, the overshadowing group should be impaired compared to the control group because the cues D and X have acquired less control over searching for the platform than in the respective control groups. This is exactly what was found, so this result provides evidence against the claim that O'Keefe and Nadel make that the formation of cognitive maps occurs

in an all-or-none fashion. In the study by Goodyear and Kamil, O'Keefe and Nadel do not differentiate between the control that is acquired by cues closer to the goal and cues more distant from the goal. As long as each cue is explored and each cue is stable within the environment, all cues should be incorporated into the map and thus no difference in the control acquired by each cue should be found. The associative theory of Rescorla and Wagner (1972) explained in Section 1.1 at first glance also has a problem with the results of Goodyear and Kamil if one assumes that all the landmarks maintain the same salience. Why should a proximal landmark overshadow a more distal landmark but not the other way around? It is possible to reconcile this result with the principles of associative learning. One could argue that landmarks closer to the goal are attended to more and thus have higher salience than more distal landmarks. According the Rescorla-Wagner (1972) model, the associative strength of the more proximal cues would then acquire associative strength at a faster rate than the less salient distal landmarks. If this assumption is correct, then one would expect that proximal cues should overshadow learning about the more distal cues to a greater extent than overshadowing of proximal landmarks by distal cues. This is consistent with the findings of Goodyear and Kamil. Similarly, the reports of overshadowing of learning about distal landmarks by a beacon by Roberts and Pearce (1997) can be explained by assuming that the beacon was higher in salience than the distal cues. Given these results, it is possible that these studies are not assessing cue competition per se, but whether animals are selectively attending to some cues and not others. However, it is hard to offer an explanation in terms of selective attention for studies that show reciprocal overshadowing (March et al., 1992; Sanchez-Moreno et al., 1999).

The evidence of overshadowing is overwhelmingly in support of the idea that spatial cues in the environment compete with each other for the control they acquire over spatial behaviour and this is the main principle of associative learning. We now turn to the

associative phenomenon of blocking to further strengthen the idea that there is no need to assume a special learning process governs spatial learning.

1.2.2. Blocking in the Spatial Domain

Blocking, as already described, is an associative phenomenon that has been widely studied and is theoretically a more sensitive test of cue competition than overshadowing. It is critical one examines the blocking literature for two reasons. First, by showing evidence of overshadowing and blocking of spatial cues it adds generality to the idea that learning in the spatial domain obeys associative principles. Second, and more importantly, blocking allows one to directly test the flexibility of the cognitive map or in other words the claim that O'Keefe and Nadel (1978) make that a cognitive map can be continuously updated. For instance, if a novel spatial cue is added to the array of pre-existing cues, that novel cue would be readily incorporated into the map. According to associative principles the addition of a novel cue would acquire very little control over the animals' spatial behaviour because it provides redundant information.

Blocking in the spatial domain has been reported in many experimental situations. For example, Roberts and Pearce (1999) trained rats in a swimming pool during Stage 1 where they were required to swim to a beacon attached to a submerged platform with a curtain surrounding the pool to restrict visual access to distal cues located on the walls of the experimental room. During Stage 2 the curtain was drawn open and the beacon and platform remained in the same place with respect to the distal cues. A control group received only Stage-2 training. During a test with the beacon and platform removed from the pool, the rats that received prior training with the beacon spent significantly less time in the vicinity of where the platform had been previously located than the control group. This outcome shows that prior establishment of a beacon as a signal for reinforcement blocked learning about

distal cues when they were both presented during the second stage of training. Moreover, blocking has been observed between intra-maze and extra-maze cues on a radial maze (Chamizo et al., 1985). All of these results suggest that spatial cues compete for associative strength in the same way as stimuli compete for associative strength in Pavlovian conditioning and as such, learning about spatial cues is incremental and not in an all-or-none fashion inconsistent with the proposal of O'Keefe and Nadel (1978).

In order to test the idea that cognitive maps are continuously updated, Rodrigo, Chamizo, McLaren and Mackintosh (1997) studied the interaction among distal landmarks. They trained rats in a swimming pool with an array of 3 distal landmarks, ABC located within a black curtain that encircled the pool. When a novel cue, X, was introduced into the pre-existing array of distal landmarks in a subsequent stage of training, rats learned very little about X. In fact, learning about ABC blocked learning about X. This result provides little support for the cognitive map hypothesis because according to this theory landmark X should have been incorporated in to the cognitive map of the environment. In contrast, associative principles predict that during the first stage of the experiment, landmarks ABC would gain control over searching for the submerged platform by acquiring associative strength. When landmark X was introduced in the second stage, only a modest amount of associative strength would be acquired by X compared to the associative strength acquired by landmarks ABC.

It is possible that O'Keefe and Nadel's (1978) cognitive map theory may be able to explain the examples of blocking described above. According to O'Keefe and Nadel exploration is crucial for the development of a cognitive map. For a landmark to be incorporated into a cognitive map it must be actively explored. It is hard to conceive how distal cues located beyond the peripheral of the pool could be explored, so it is possible that the novel cue introduced at the outset of Stage 2 may not be explored and as a result of this would not be incorporated into a cognitive map. Biegler and Morris (1999) speak to some

extent on this matter. They conducted a blocking experiment in which rats were required to find food with reference to a particular array of landmarks that were located within the experimental arena. For an experimental group, rats were initially trained to locate food with reference to a single landmark located 100 cm from the food. During this stage, a control group was trained to find the goal with reference to a different landmark. In a subsequent stage, the experimental group received the same training to that received in Stage 1 except an additional landmark was added to the arena located 50 cm from the food. The control group received the same training as the experimental group during the second stage. During single landmark tests, the landmark introduced at the start of Stage 2 acquired less control for search for the food location in the experimental group than in the control group. This result shows a clear blocking effect. However, Biegler and Morris also conducted tests on the first trial of Stage 2 in which they recorded time spent in a 40-cm diameter circular search zone located with the landmark at the centre of the zone. They found that rats in both groups increased their time significantly around the landmarks. In this study, one landmark blocked learning about another landmark even when rats explored, and presumably had the opportunity to incorporate the novel landmark into a cognitive map. This study further questions the existence of cognitive maps and supports previous findings of blocking in the spatial domain.

From the information presented on blocking and overshadowing in the spatial domain it is clear that spatial learning obeys associative principle, consistent with associative theories of learning. Finally, an evaluation of landmark stability will be discussed in the following section.

1.2.3. Landmark Stability

According to O'Keefe and Nadel (1978), 'variability' is a major determinant of whether landmarks will be incorporated into a cognitive map. It then follows that if the

position of a landmark is perceived to be unstable with respect to a stable global framework, then the landmark is essentially ignored. In contrast, associative theories of learning predict a very different outcome. As long as the landmark maintains its spatial relationship with the goal, the landmark will gain associative strength and come to control the animals' behaviour, even if the landmark is unstable with respect to a global frame of reference.

Biegler and Morris (1993) initially tested the idea that landmark stability is essential for successful spatial learning by training rats in a square-shaped open field surrounded by three black curtains and one white curtain. The white curtain acted as a polarizing cue which rats could use to acquire their orientation and directional information. Within the open field, two groups of rats were trained. Group fixed was trained with two different landmarks always in the same position with respect to the global framework, while a second group, group varied, was trained with the same two landmarks, but the positions of the landmarks were random across training. In both groups a food pellet was always located 40 cm due South (in relation to the white curtain) from one of the landmarks. A test trial in the absence of the food revealed that group fixed spent more time searching at the location where the food was located during training, while group varied spent more time searching around the appropriate landmark rather than the correct direction and distance from the landmark. According to Biegler and Morris, group fixed had incorporated both landmarks into a map of the environment, and thus could use the landmarks along with the frame of reference to search accurately for food in the appropriate location, but in group varied, since the landmarks were unstable, they were not incorporated into the map and thus the location of the food could not be determined accurately with reference to the landmark.

There are multiple problems with Biegler and Morris' (1993) experiment which they acknowledged in a subsequent report (Biegler & Morris, 1996). In their initial experiment (Biegler & Morris, 1993), group fixed had multiple sources of directional information that

could have been used, including the white curtain, and a second irrelevant, but stable, landmark. Group varied only had the white curtain, since the second landmark was randomly moved across trials. The additional directional information may have helped group fixed in locating, more accurately, the location of the food during testing and thus have produced the results that were obtained. To correct this problem, Biegler and Morris (1996) conducted an experiment with a single landmark. Groups fixed and varied were trained as before, but only a single landmark was ever presented during training. In this instance, during testing in the absence of the food, both groups spent more time searching in the location where the food was located during training, but there appeared to be more localised search and hence more time spent searching at the food location in group fixed compared to group varied. The very fact that rats in group varied learned the position of the food casts doubt on the claim that stability is a prerequisite for the formation of a cognitive map (O'Keefe & Nadel, 1978). However, the fact that group varied spent less time at the food location than group fixed is also troubling for associative theories of learning that would predict the opposite result. In group varied the landmark is the sole predictor of the location of food and as such should acquire greater control over searching for the food than in group fixed. Performance in group fixed should suffer due to the stable global framework and the stable landmark overshadowing each other.

Overall, the results of Biegler and Morris (1996) are difficult to interpret because the majority of tests were conducted in the presence of both the landmark and the polarizing cue (white curtain). For the most part all test trials examined the control that was acquired by the landmark in the presence of the polarizing cue and thus an independent measure of the control of the landmark was not obtained except from one test. In that test (Experiment 2; Test 6) only the landmark was present and the polarizing cue was absent. For the results of this test, Biegler and Morris stated that "with both polarizing and vestibular cues absent,

search was no longer focused in any one direction” (p. 331). This pattern of results would be expected, but if anything learning the significance of the landmark should reveal itself by rats searching in a circular region at the appropriate distance around the landmark. Unfortunately, the statistical analyses are not clear but just from observing the representative paths traveled by the rats during this test, group varied had a more circular search than group fixed, which appears more random. Given this pattern of results, it appears more control over spatial behaviour was acquired by the landmark in group varied than in group fixed which would go against the initial conclusion that was drawn from these experiments. However, this conclusion is based solely on observation of the paths taken by the rats during this test that were presented in the article and so must be taken with caution.

Two additional studies have examined whether spatial learning is successful with unstable landmarks. Collett, Cartwright and Smith (1986) conducted a simple experiment in which gerbils were required to find food located 50 cm due South of a landmark. The food location was always in a consistent place with respect to the landmark, but the landmark (and therefore the food) were moved randomly across trials. During a test trial in the absence of the food, the gerbils spent a large proportion of their time in the correct location where the food was located during training. It is unclear how the gerbils knew which direction the food was located as there was no polarizing cue within the apparatus. It is possible that unidentified room cues were perceived by the animals and they acquired their directional information from them. Another possibility is that on being carried from the holding room to the apparatus, gerbils attained their orientation from a sense of direction that is thought to guide path integration (Etienne, Teroni, Maurer, Portenier & Saucy, 1985; Mittelstaedt & Mittelstaedt, 1980). No matter how they gained their orientation, it is clear that gerbils used the unstable landmark and its distance from the landmark to search for the food at the correct location. There are two problems with this experiment. First, Collett et al. (1986) did not

have another group that received the landmark in a stable position so conclusions drawn on the relative importance of landmark stability cannot be made. Second, it is possible that the landmark was not perceived as being unstable as it is unclear in the report where this information comes from. One could predict that the apparatus boundaries may serve this function but it is possible that the boundaries were not noticed by the animals as they were left “in shadows” (p. 837). Roberts and Pearce (1998) address both of these concerns in the following experiment.

Roberts and Pearce (1998) conducted a series of experiments investigating the control acquired by unstable landmarks in a swimming pool task. In one experiment, two groups of rats were trained in a swimming pool that was surrounded by distal landmarks that provided a global frame of reference. In one group, a hidden platform was always located 30 cm due south of a landmark, which remained in a constant place with respect to the distal cues. A second group was trained similarly to the first group but the landmark and the platform moved randomly within the pool across sessions (4 trials per session), but maintained their relationship with each other. Both groups then underwent an extinction phase in the presence of the distal landmarks but the landmark and platform were absent from the arena. This phase was conducted to reduce control acquired by the distal landmarks in both groups. Following the extinction phase, both groups received a single trial that was conducted in the same manner as previous training trials except the platform was either in a novel location (Roberts & Pearce, 1998; Experiment 4) or familiar place (Roberts & Pearce, 1998; Experiment 5). In both experiments, rats took significantly longer to find the platform when the landmark was in a fixed location than when the landmark varied positions during training. Similarly, significantly more rats in the fixed conditioned failed to find the platform during the test trial than in the varied condition. These results are in complete contrast to Beigler and Morris’s (1993; 1996) results that showed more control acquired by the landmark in the

fixed condition than the varied condition. Clearly, the claim by O'Keefe and Nadel (1978) that 'variability' disrupts spatial navigation based on the cognitive map cannot account for the results reported by Roberts and Pearce, however, these results are in complete agreement with associative principles. In the fixed group, because both the distal cues and the landmark were relevant predictors of the goal during training, it is expected that each one would restrict learning about the other. In the varied group, the distal cues were irrelevant thus the only reliable cue that could have been used to find the submerged platform was the landmark. Greater associative strength should have been acquired by the landmark in the varied group than the fixed group and thus resulted in the fixed group taking longer to find the platform during the test trial than the varied group.

Biegler and Morris' (1993) claim that, "if it moves, don't use it as a landmark" (p. 633), does not appear to withstand experimental testing. With better controlled experiments (e.g., Roberts & Pearce, 1998) it appears that learning about landmarks obeys associative principles rather than the principles that govern the formation of cognitive maps.

1.2.4. Is There a Need for a Cognitive Map?

There is a need to return briefly to the question of whether it is necessary to postulate two distinct learning systems such as the taxon system and locale system (O'Keefe & Nadel, 1978), for learning in the spatial domain. From the previous sections of this thesis, it is abundantly clear that the evidence from spatial cue competition studies (e.g., overshadowing and blocking), suggests that associative learning theories (e.g., Rescorla & Wagner, 1972) account for the experimental results much more comprehensively than does the principles that govern the formation of a cognitive map (i.e., learning in the locale system). There is, however, one concern that deserves some comment. For the studies that found overshadowing (Chamizo et al., 1985; March et al., 1992; Redhead et al., 1997) and blocking

(Chamizo et al., 1985; Roberts & Pearce, 1999) between intra-maze (e.g., surface cues, local landmark and beacons) and extra-maze cues (e.g., distal landmarks), there is a possibility that O'Keefe and Nadel's (1978) account of spatial learning may be able to reconcile these results with their theory. The studies that looked at overshadowing and blocking between intra-maze and extra-maze cues are essentially looking at the interaction between the taxon and locale systems. It is unclear how O'Keefe and Nadel envision these two systems interacting. All they offer on this matter is that they "cannot specify precisely the factors controlling hypothesis [strategy] selection" (p. 92). Given the results that strongly suggest that overshadowing and blocking occur between these two navigational systems then it seems reasonable to conclude that this interaction is controlled by a competitive learning process as suggested by associative theories of learning (e.g., Rescorla and Wagner, 1972). If this is correct then many of the above findings would be compatible with the proposal of O'Keefe and Nadel.

Given the ambiguity of the initial results of cue competition in the spatial domain, it was important to further evaluate the literature that looked at overshadowing and blocking among distal landmarks that would all be represented by the locale system. For example, in an experiment in which the landmarks were located varying distances from the goal, the closer landmarks overshadowed learning about the more distal ones (Goodyear & Kamil, 2004) See also Rodrigo et al. (1997) and Sanchez-Moreno et al. (1999). These studies clearly show that associative principles better explain the interaction between distal landmarks than the principles that govern the formation of cognitive maps.

It is also possible to criticise the idea that animals form a cognitive map. If they do not form a map then it is not clear why spatial learning should not be governed by the principles of associative learning. First, if an animal is thought to have acquired a cognitive map, then it is expected to be able to make novel trajectories to the goal (O'Keefe and Nadel,

1978). However, evidence suggests animals actually find it very difficult to take truly novel trajectories when navigating (e.g., Alyan, 1994; Bennett, 1996; Sutherland, Chew, Baker, & Linggard, 1987). For instance, Sutherland et al. (1987) trained rats in a swimming pool to locate a hidden platform with reference to an array of distal landmarks. During training rats were restricted to only one half of the pool by the presence of a clear Perspex divider. During tests, the Perspex divider was removed and rats were released from the previously restricted section of the pool (and thus a truly novel path was required to find the platform). Rats that were released from the novel start location took longer to find the platform than a group that had physical and visual access to the entire pool during training. Such a finding suggests that rats in the restricted access group were unable to make use of a map in order to head directly to the goal.

Second, Pearce, Good, Jones, and McGregor (2004) trained rats to locate a hidden platform positioned near one corner of a rectangular swimming pool. During four transfer sessions (4 trials per session), rats were placed in a kite-shaped pool with the platform either in a corner that had the same geometric properties as the correct corners in the rectangle (a consistent group) or in a corner that had the same geometric properties as the incorrect corners in the rectangle (an inconsistent group). The consistent group was superior to the inconsistent group at finding the platform in this test stage of the experiment. This result suggests that animals were not encoding global spatial information as suggested by O'Keefe and Nadel (1978), but relied on local spatial information such as searching in a particular corner with particular properties to find the platform (See also, McGregor, Jones, Good, & Pearce, 2006).

O'Keefe and Nadel's (1978) idea that there is a special learning process for spatial learning does not hold up under close inspection. Simple associative principles have been able to explain quite clearly all the results including overshadowing, blocking, and landmark

stability in the spatial domain thus far. Moreover, the evidence for the existence of cognitive maps is not compelling. There is however another important consideration that must be addressed and that is how rats learn to locate a goal with reference to a geometric representation of an environment. It has been argued that learning in these circumstances is special and does not adhere to the principles of associative learning (Cheng, 1986; Gallistel, 1990). Is this correct, or can associative principles provide an adequate explanation for these results as well?

1.3. Is Spatial Learning Special: II. Geometric Module Considerations

Animals are thought to use geometric cues whilst navigating through their natural environment. Geometric cues can be provided by the environment in two ways. First, geometric cues can be provided by the arrangement of specific landmarks (Greene & Cook, 1997; Benhamou & Poucet, 1998). Second, and more common in the experimental setting, the geometric cues are provided by the shape of the training arena. How animals learn about geometric cues is of particular interest because, just like the idea that animals form a cognitive map of their environment, there are those that suggest a similar specialised process for learning about geometric cues. In particular, Cheng (1986) and Gallistel (1990) are both supporters of this idea and have conceptualised learning about geometric cues as a specialised learning process that occurs within an encapsulated geometric module that is resistant to non-geometric information. In contrast, if the principles of associative learning theory apply to learning about geometric information, then the rules that govern learning about geometric and non-geometric information should follow a competitive learning rule, inconsistent with Cheng and Gallistel's claim that geometric and non-geometric information do not interact. Prior to identifying the process by which geometric cues are learned about, a working definition of what is meant by geometric cues is needed.

The geometry of an environment consists of two components, metric and sense properties (Gallistel, 1990). The metric properties refer to the computation of distances and angles while the sense properties refer to the distinction between left and right. Both metric and sense properties are needed to locate unambiguously a goal in an enclosed arena. Take for example an arena with a rectangular shape. Each corner of a rectangle is constructed from a short and a long wall forming a 90° angle. With just this metric information, each corner would be perceived as equivalent. However, if sense information is included, then there are two distinct geometric locations, two corners where the short wall is to the left of the long wall and two corners where the short wall is to the right of the long wall. Thus whenever the term geometric cues is used, it refers to both the metric and sense components of geometry.

1.3.1. The Geometric Module

Cheng (1986) conducted a set of influential experiments in a rectangular arena with distinct featural cues (colour, texture, luminance, and odour) located in each of the corners. In a working memory paradigm of this task, animals were placed in the arena and allowed to find a reward located in one of the corners. The rats were then removed from the apparatus and had a delay period of 75 s before being placed back into the same environment with the food in the same location as the first trial. The position of the food changed daily. Cheng observed that rats chose equally between the two corners with equivalent geometric properties, essentially ignoring the featural cues that provided information to the exact location of the reward. In a reference memory version of this task, rats were trained to locate a reward that was always located in the same place. When the rats were tested in the environment in the absence of reward, they made choices to the correct corner 71% of the time and made errors to the diagonally opposite corner (the geometrically identical corner),

only 21% of the time. From this result it was clear that the rats were capable of using featural cues to disambiguate the two geometrically identical corners, but when the featural panels at the two correct corners were removed, choices between these two locations became the same. Even though the featural panels at the remaining two corners could have been used by the rat to disambiguate the two corners, they failed to do so suggesting that rats tend to use geometric cues even though they are redundant and less valid than the featural cues. From these empirical results, Cheng proposed that animals have a geometric module.

Cheng (1986) and Gallistel (1990) proposed that in the mind (Cheng, 1986) or brain (Gallistel, 1990), animals have a geometric module that encodes geometric information; encoding what they referred to as a metric frame that includes both metric and sense information. Gallistel (1990) further suggested that the geometric module was impenetrable to non-geometric information suggesting that the module “takes no account of the smells, emanating from surfaces, their reflectance or luminance characteristics, their texture, and so on” (p. 208). It must be noted that Cheng’s (1986) initial theory did not claim that the geometric module was impenetrable to non-geometric information. To account for the results that clearly showed rats learned to use featural information to disambiguate between two geometrically identical locations, Cheng (1986), later extended in Cheng and Newcombe (2005), suggested an alternative way in which animals use geometric and non-geometric information. In one version of this theory, geometric and non-geometric information are initially encoded in independent modules that do not interact. At some point, which is unclear, the two modules may be integrated in a higher order memorial system. Features are linked to the metric frame with address labels, but this integration or cross talk between the two modules may not always occur. This occasional failure to integrate information can result in animals disregarding featural information, as in the working memory experiment. In other instances, featural information can be ‘pasted’ onto the metric

frame and thus a decision based on the metric frame allows the animals to correctly choose the correct location, as in the reference memory experiment. This form of the model allows for an interaction between geometric and non-geometric information but it is unclear when and where this interaction takes place. Also, the initial encoding of geometric and non-geometric information is still said to occur in independent modules which suggests an aspect of impenetrability, at least in the early stages of his model, with the information for each module being encoded in parallel and not in a competitive manner.

This idea that geometric information is encoded in an encapsulated module that is resistant to the influences of non-geometric information suggests that there is something unique about geometric cues. Unique in that, if there is a geometric module, geometric cues should not compete with other cues in the environment for control over spatial behaviour in environments with a distinctive shape. We have already seen that spatial cues, including local landmarks, beacons, and distal landmarks, do compete for control over spatial learning, so is it really the case that geometric cues are different? As the following section will highlight, the proposals of Cheng (1986) and Gallistel (1990) concerning the geometric module has stood for almost 20 years without being challenged. However, in the recent years, research has shown that the geometric module is not impenetrable to non-geometric information.

1.3.2. Early Support for the Geometric Module

Early support for the claim that the geometric module is impenetrable to non-geometric information came from experiments conducted along the same lines as Cheng's (1986) initial experiments. In these experiments, animals were tested for their ability to locate a hidden goal by reference to geometric cues provided by the shape of the arena. The procedures are almost identical to those employed by Cheng (1986), so there is no point in

rehashing them here, and the results do not differ much except for a few exceptions. Like Cheng (1986) it has been found that animals predominately use geometric cues to make choices in an arena with a distinctive shape. This effect has been shown in a variety of species such as fish (Sovrano, Bisazza, & Vallortigara, 2002; 2003), chicks (Vallortigara, Zanforlin, & Pasti, 1990), pigeons (Kelly, Spetch, & Heth, 1998), rhesus monkeys (Gouteux, Thinus-Blanc, & Vauclair, 2001) and human children and adults (Hermer & Spelke, 1994; Wang, Hermer, & Spelke, 1999), generally with a reference memory task.

All of the aforementioned studies have shown that animals can use the shape of the environment to find a hidden goal even when more reliable and valid non-geometric cues are present. This has been taken as evidence for the presence of a geometric module that encodes a metric representation of the environment in an almost incidental manner. However, all of these studies lacked proper control groups to test the nature of the interaction between geometric and non-geometric cues. It is not clear whether learning about geometric cues in these studies was restricted due to the presence of non-geometric cues during training because no control group was trained with just geometric cues relevant. Do geometric and non-geometric cues compete with each other, consistent with the principles of associative learning, or do animals truly learn about geometric cues irrespective of the presence of other cues? The next section explores some experiments that include the appropriate control conditions to directly test whether geometric and non-geometric cues interact, but as we will see, these studies are consistent with Cheng's (1986) claim that learning about geometric information is not influenced by the presence of non-geometric information.

1.3.3. Further Support for the Geometric Module – Cue Competition Studies

In the swimming pool, a number of studies have shown that a local landmark either attached to a submerged platform (Pearce, Ward-Robinson, Good, Fussell, & Aydin, 2001) or

near the platform (Hayward, Good, & Pearce, 2004; Hayward, McGregor, Good, & Pearce, 2003) failed to overshadow and block learning about the location of the platform with respect to the shape of the environment. For instance, Pearce et al. (2001; Experiment 3) trained rats to locate a platform in one of the corners at the base of an isosceles triangular-shaped pool. The overshadowing group was trained to locate a platform in one of the corners of the triangular pool, in which a landmark was always attached to the platform. The control group received the same training, except the landmark was absent. Following training, rats were tested in a triangular pool with the platform and landmarks removed. The overshadowing and control groups spent an equal proportion of time searching in the vicinity of where the platform was located during training. This finding suggested that the landmark did not restrict learning about the location of the platform with respect to geometric cues.

Similarly, in an appetitive paradigm, Wall, Botly, Black, & Shettleworth (2004) initially trained rats in a square-shaped arena. A blocking group received a baited food bowl in one of the corners of the square with black panels signalling the location of the food. At the remaining corners in the square an unbaited food bowl was present. A control group of rats received the same training except the black panels were absent from training and they simply received a single baited bowl present in one of the corners. The location of the baited bowl was random across trials. In a subsequent stage of training, the blocking and control groups were trained to locate food in one corner of a rectangular arena, with black panels also signalling the location of the reward. Following this stage of training, tests were conducted in a rectangular arena in the absence of the black panels and any food. The blocking and control groups made 83% and 75% choices to the correct corners, respectively, and this difference was not significant. These results suggested that the presence of the black panels did not block learning about the significance of geometric cues.

A powerful example of a failure to find overshadowing of geometric cues by non-geometric cues in an appetitive paradigm comes from Kelly et al. (1998). A geometric group was trained to find food in one corner of a rectangular enclosure with absolutely no featural cues present. A feature group was trained in the same manner except that at each corner there was a distinct featural panel. During test trials featural cues and the food were absent from the environment. The geometric group made correct choices to the correct corner on 93% of the test trials compared to 88% in the feature group. This experiment is a particularly good demonstration of the failure of non-geometric cues to overshadow geometric cues because one would expect that the feature group would experience greater generalisation decrement from training with the features present to testing without the features. The geometric group would not experience such a change. It then follows that the feature group would be slightly impaired during test trials because of the change experienced from training to test trials and thus may have produced an overshadowing effect. Since Kelly et al. found no significant difference in the percentage of correct choices on test trials between the groups then one can conclude that non-geometric cues did not overshadow at all, geometric cues.

All of the above experiments have shown failures to find cue competition in the spatial domain specifically when geometric cues are involved. There are at least two possible explanations for why non-geometric cues failed to overshadow geometric cues. First, the results can be explained by associative learning theory if it is assumed that there was a difference in the salience of the two types of cues. According to the Rescorla-Wagner (1972) theory, the likelihood of detecting an overshadowing influence of the non-geometric cues over the geometric cues will be reduced when the salience of the former is substantially less than that of the latter. This explanation, although plausible, is unlikely. Hayward et al. (2003; Experiment 2) conducted a study to evaluate whether geometric cues are greater in salience than a landmark. They trained two groups of rats to locate a hidden platform in a

triangular arena. For one group, the platform and a spherical landmark located 60 cm from the platform moved randomly between the two corners at the base of the triangle across trials. To solve this task, animals could only find the platform with reference to the landmark and not geometric cues. In the other group only the landmark moved randomly between the two corners and the platform remained in the same corner across trials. For this group, rats could only find the platform with reference to geometric cues. At the start of training, both groups initially made approximately 50% correct choices to the corner that contained the platform. By the end of training, the group that had to rely solely on the landmark were making approximately 80% correct choices compared to 60% in the group that had to rely on geometric cues for finding the platform. These results suggest that, if anything, the landmark had greater salience than the geometric cues thus it is unlikely that the failure to find overshadowing of geometric cues by non-geometric cues is a result of the difference in relative salience between geometric and non-geometric cues.

A second explanation for the failure to find overshadowing of geometric cues by non-geometric cues, and generally the conclusion that was drawn from these experiments, is that animals encoded geometric cues independently of any other cues via some sort of geometric module (Cheng, 1986). Does this mean, therefore, that geometric cues are unique in that they do not compete with other spatial cues for behavioural control over spatial learning in environments with a distinctive shape? A recent set of experiments demonstrating potentiation, blocking and overshadowing in a rectangle (Graham, Good, McGregor, & Pearce, 2006; Pearce, Graham, Good, Jones, & McGregor, 2006) suggest otherwise. Also, Miller and Shettleworth (2007) recently developed an associative model of learning in environments with a distinctive shape that reconciles the failures to find overshadowing and blocking of geometric cues by non-geometric cues by appealing to associative principles.

1.4. Potentiation, Overshadowing, and Blocking In Environments with a Distinctive Shape

Graham et al. (2006) conducted a detailed investigation on the effects of learning about geometric cues when the shape of the environment provided geometric and non-geometric information. They trained rats in a kite-shaped swimming pool. Two groups of rats were trained to locate a hidden platform located in one of the right-angled corners of the kite. For a shape + colour group, this corner was always constructed from two adjacent black walls, while the opposite corner was constructed from two white walls. For the shape only group, the platform remained in the same corner with respect to geometric cues, but the colour of the two walls creating the corner were black on half of the trials and white for the remaining trials (see Figure 1.1). After training was completed, all rats were given a 60-s test trial in an all black kite, with the platform removed. The shape + colour group spent approximately 60% of their time searching in the vicinity of where the platform was located during training, while the shape only group spent significantly less time, approximately 40%, in the correct quadrant of the pool. It is clear that the presence of reliable coloured walls potentiated learning about geometric cues, in the kite-shaped arena, or that the alternating coloured walls disrupted learning in the shape only group. This latter explanation was challenged by the results of a subsequent, similar, experiment which included a group that was trained in the same manner as the shape only group except that training took place in an environment of a uniform colour, the shape + no colour group. During a test in the absence of the platform and any informative coloured cues, there was no difference between the proportion of time spent in the vicinity of where the platform was located during training between the shape only and the shape + no colour groups, and both of these groups spent significantly less time in the correct quadrant than the shape + colour group. Potentiation of learning about geometric cues was still observed.

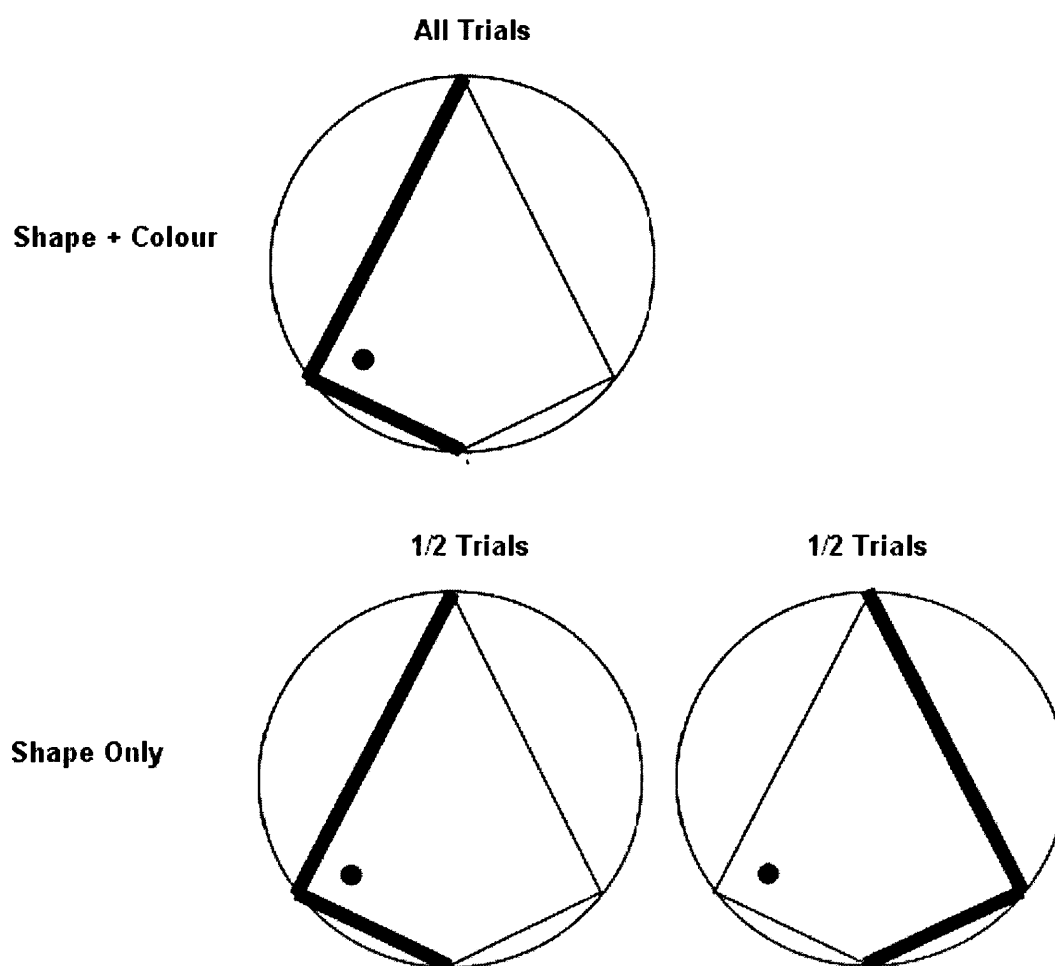


Figure 1.1. Schematic representation of the training conditions for the shape + colour and shape only groups in the experiment by Graham et al. (2006). The shape only group received two trial types intermixed. The black circle represents the submerged platform.

Potentiation of geometric cues provides problems for both the idea that animals encode geometric cues in a dedicated module (Cheng, 1986; Gallistel, 1990) and current associative theories (e.g., Rescorla and Wagner 1972). On one hand, Cheng's and Gallistel's theory suggests that non-geometric cues such as coloured walls should not influence learning about geometric cues in any way because of the supposed impenetrability of the module to non-geometric information. However, it is clear that learning about non-geometric cues does indeed interact with learning about geometric cues. On the other hand, the nature of this interaction is not one that is envisioned by learning theories such as the Rescorla-Wagner theory. In fact, the Rescorla-Wagner theory would predict overshadowing of geometric cues by wall colour rather than potentiation. I shall return to this issue in Chapters 5 and 6 where an associative learning explanation of potentiation in a spatial task is based on the formation of between-cue associations.

Further evidence that learning about geometric cues and landmarks influence learning about each other comes from a study conducted by Pearce et al. (2006). They replicated the result of the previous study that showed that by making the walls of the correct and incorrect corner different colours in a kite, learning about geometric cues was potentiated. Interestingly, potentiation of learning about geometric cues by coloured walls was not found in a rectangular environment. In fact, overshadowing and blocking of geometric cues by coloured walls was found. For example, Pearce et al. trained three groups of rats to locate a hidden platform in one corner of a rectangular pool. For an experimental group, this corner was constructed from two adjacent white walls, and the diagonally opposite corner was constructed from two adjacent black walls. One control group was trained in an all white rectangle and the other control group was trained in a rectangle but the correct corner was constructed from two black walls on half of the trials and two white walls on the other two trials (see Figure 1.2). A 60-s test trial was conducted in a rectangle constructed from four

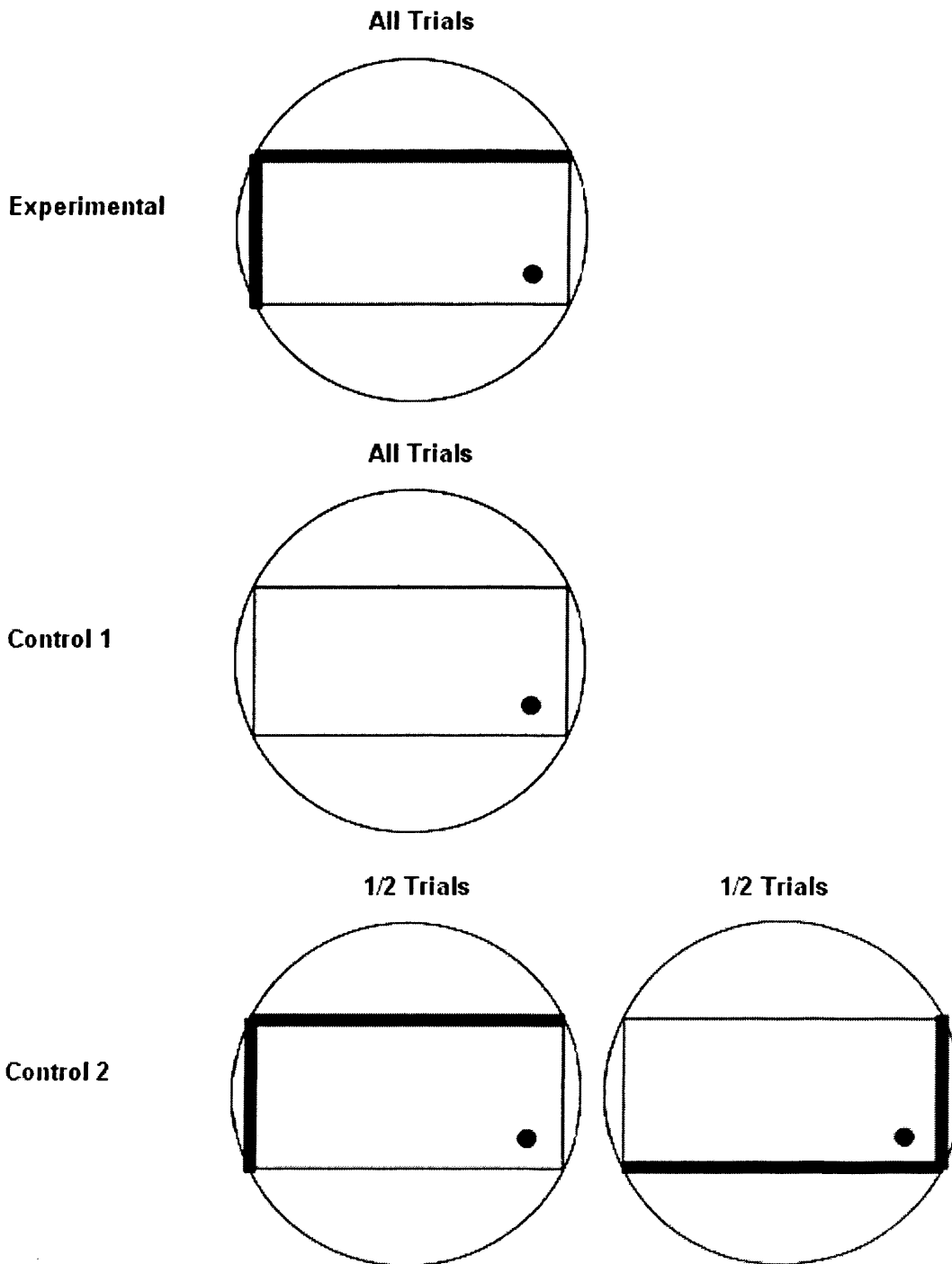


Figure 1.2. Schematic representation of the training conditions for the three groups in the experiment by Pearce et al. (2006). The control 2 group received two trial types intermixed. The black circle represents the submerged platform.

white walls and in the absence of the platform. This test revealed that the control groups spent a greater proportion of time in correct quadrants compared to the experimental group. It is clear that in the experimental group the coloured walls overshadowed learning about geometric cues. In an earlier study, overshadowing of geometric cues by a coloured wall was also found. Gray, Bloomfield, Ferrey, Spetch, and Spurdy (2005) trained mountain chickadees to search for a food reward located in one corner of a rectangular arena. In a geometry group, searching for food was conducted in a rectangle in the absence of any coloured cues. In a near-feature group, the long wall adjacent to the food location was blue. During test trials in the rectangle in the absence of the blue wall and any food, the geometry and near feature groups made 84% and 56% of their choices, respectively, to the corner that contained food during training and the diagonally opposite corner (the geometrically identical location). Clearly the presence of the blue wall, just as the coloured walls in Pearce et al., disrupted learning about geometric cues.

These three studies described above (Graham et al., 2006; Gray et al., 2005; Pearce et al., 2006) provide the strongest empirical evidence to date against the idea that learning of geometric information is not influenced by non-geometric information (Cheng, 1986). Recently, in a review article, Cheng (2008) retracted his theory of a purely geometric module. In light of the new empirical evidence, Cheng stated that “a pure geometric representation devoid of featural cues seems unlikely” (p. 360). This then leaves researchers to provide alternative theories of navigation in environments with a distinctive shape. Of particular interest to the present discussion is the model of Miller and Shettleworth (2007; 2008). They have provided an associative model of learning about geometric cues that was intended to explain the failures to find cue competition between geometric cues and non-geometric cues as well as successful demonstrations of potentiation described earlier. However, there remain

some problems associated with this model that need to be addressed, which is, in part, the goal of this thesis.

1.5. An Associative Model of Geometry Learning (Miller & Shettleworth, 2007)

Miller and Shettleworth's (2007) goal for developing an associative model of learning about geometric cues was to develop a theory to explain the conflicting results that were observed with cue competition between geometric and non-geometric cues. As was previously discussed, in some environments landmarks at or near the goal failed to block and overshadow learning about geometric cues (Hayward et al, 2003; Hayward et al, 2004; Pearce et al, 2001; Wall et al. 2004), while in other environments, featural cues successfully overshadowed (Gray et al., 2005; Pearce et al, 2006), blocked (Pearce et al., 2006), and potentiated (Graham et al., 2006; Pearce et al., 2006) learning about geometric cues.

The general concept of the model is identical to the Rescorla-Wagner (1972) model. Miller and Shettleworth (2007) suggested that environments with a distinctive shape are composed of elements, including geometric and featural cues at different locations. These cues gain and lose associative strength according to the rules set forth by Rescorla and Wagner. Take for example a triangular swimming pool shown in the top-left panel of Figure 1.3, with a platform and landmark located in the correct corner. There are five distinct elements in the environment that have zero associative strength at the beginning of training except the common cue which is assumed to have an initial associative strength of 0.1. At the correct location – where the platform is placed – there is the geometric cue of the correct corner, G_C , a landmark, F , and a common cue, B . At the incorrect location, there is the geometric cue of the incorrect corner, G_I , and a common cue, B . At the apex there is the geometric cue of the apex, G_A , and the common cue, B . As a rat chooses a corner, the associative strength of each element at that location changes according to Equation 1.2,

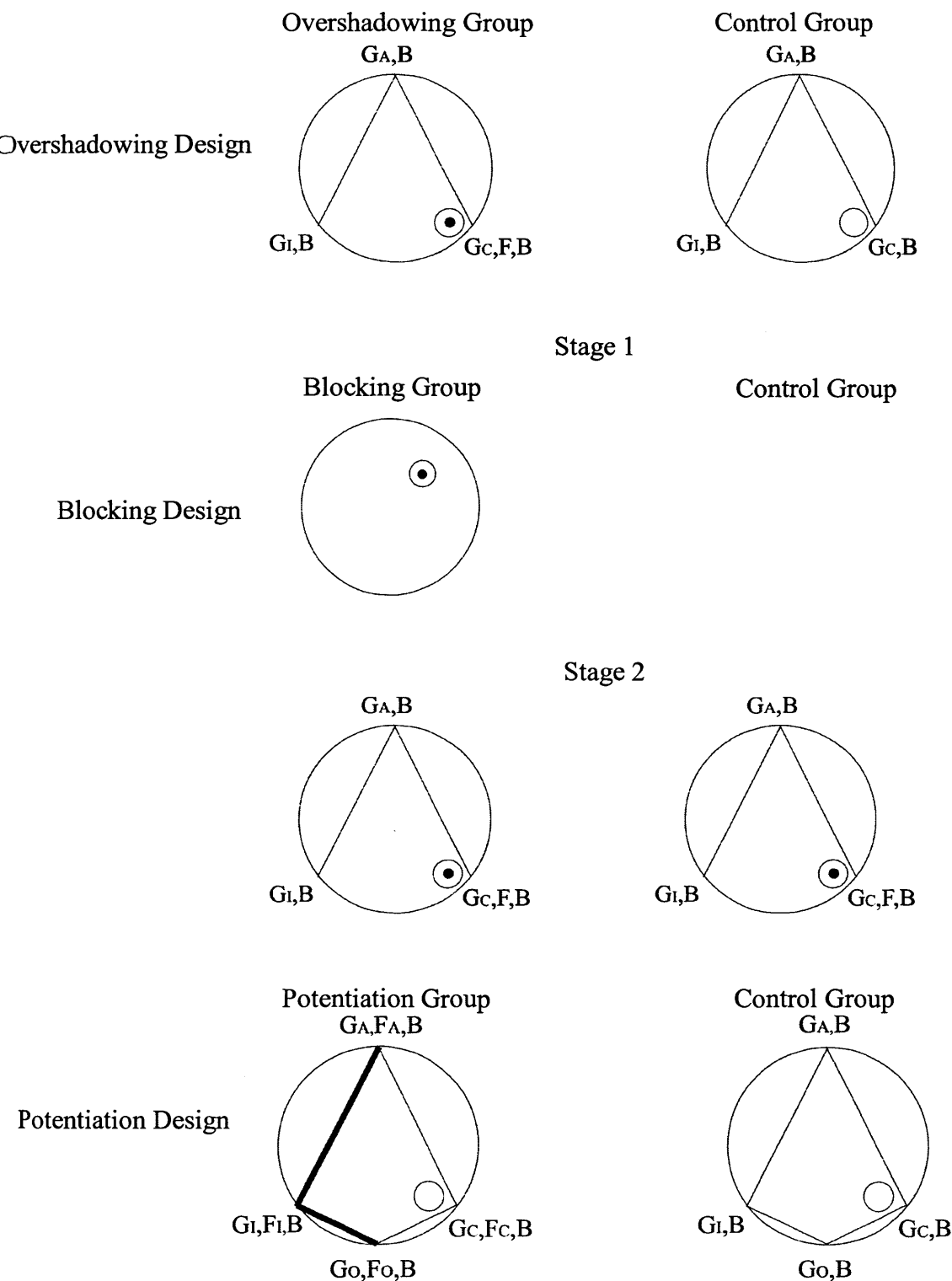


Figure 1.3. A schematic representation of typical overshadowing, blocking and potentiation designs in a swimming pool with the elemental components that Miller and Shettleworth (2007) suggest form each environment. The small white circle represents the platform and the black circle represents a landmark. G_C , G_I , G_A , G_O are the geometric cues at the correct, incorrect, apex and obtuse corners, F is the landmark, and B is the common cue.

which is based on the Rescorla-Wagner model. ΔV_E is the change in the associative strength of an element, α represents the inherent salience of the element, β and λ are the learning rate parameter and asymptotic value respectively pertaining to the unconditioned stimulus, and V_L is the sum of the associative strengths of the elements at the location in question.

$$\Delta V_E = \alpha\beta(\lambda - V_L) \quad (\text{Equation 1.2})$$

Given the operant nature of the swimming pool task, the forgoing equation was in need of adjustment. In the swimming pool, on every trial the rat is allowed to find the platform and in doing so may visit multiple locations; taking many paths to find the goal. Thus the model incorporated a probability measure of choosing any particular location, P_L , as shown in Equation 1.3, where V_L is the overall associative strength of the location in question and $\sum V_L$ is the sum of all the associative strengths of all the elements at all the locations.

$$P_L = \frac{V_L}{\sum V_L} \quad (\text{Equation 1.3})$$

By way of example, to calculate the change in associative strength on a particular trial of the common element (B) that is located at all three locations in a triangular swimming pool as shown in the top-left panel of Figure 1.3, Equation 1.4 is used. The value for α for all elements is assumed to be 0.04 and β is assumed to be 1¹. λ is always 1 when the platform is present and 0 when it is absent. The probability of selecting the incorrect corner, P_I , and the apex, P_A will vary according to Equation 1.3, however, the probability of choosing the correct corner, P_C is always equal to 1 because on every trial the rat finds the platform in the correct corner. V_{LC} , V_{LI} and V_{LA} represent the sum of the associative strengths of all the elements present at the correct, incorrect, and apex locations.

¹ Miller and Shettleworth (2007) claim that β on non-reinforced trials is normally lower than that on reinforced trials. However, they claim that since “US-mediated effects have not generally been tested in geometry-learning experiments” (p. 193) its effect was ignored. If this assumption is incorporated into their model it has no effect on the pattern of results.

$$\Delta V_B = \alpha\beta(\lambda - V_{LC})P_C + \alpha\beta(\lambda - V_{LI})P_I + \alpha\beta(\lambda - V_{LA})P_A \quad (\text{Equation 1.4})$$

For elements located at only two locations or at a single location, the above equation remains the same except only the locations at which the element is present is included in the equation. During test trials when the platform and landmarks are removed from the pool, Equation 1.3 can be used to determine the probability of choosing the correct corner given the associative strengths of each element that is present during the test (e.g., B, G_C, G_A, and G_I). It should be noted that the model is a deterministic model, meaning that the choice behaviour is assumed to be an average of a group of animals rather than a mean of individual animals. As the model stands, it incorporates no measure of variance that would be seen in an empirical study.

The model described above is Miller and Shettleworth's (2007) version as it pertains to swimming pool tasks. They refer to this version as the multiple choice model, because rats in the swimming pool may make multiple choices on any given trial before the goal is found. This is compared to the single choice model for appetitive tasks where animals usually make only one choice before being removed from the apparatus. Although somewhat different in the procedure of the tasks, the same logic that is applied to the multiple choice model is applied to the single choice model. As all the experiments in the present thesis are conducted in a swimming pool use procedures that require the multiple-choice model for their analysis, there is no need to explain the single-choice model in detail. Rather, a description of how Miller and Shettleworth's multiple-choice model accounts for the failure to find overshadowing and blocking of geometric cues, as well as successful potentiation of geometric cues in the swimming pool will be described in the following sections.

1.5.1. Failure to Find Overshadowing of Geometric Cues-Miller & Shettleworth (2007)

To describe how Miller and Shettleworth's (2007) model explains overshadowing of geometric cues by non-geometric cues a concrete example will be used. Take the simple overshadowing experiment in the swimming pool, shown in the top row of Figure 1.3. An overshadowing group is trained to locate a submerged platform in one of the corners at the base of the triangular-shaped pool. A landmark is always positioned at the goal location. A control group receives identical training in the absence of the landmark. The left-hand panel of Figure 1.4 shows the cumulative associative strength for each element in both the overshadowing and control groups across training. Miller and Shettleworth predict that when a rat enters the correct corner, the presence of the landmark (F) will restrict gains in associative strength to the geometric cue at the correct corner (G_C). Given this, it might be expected that during test in the absence of the landmark, the overshadowing group will choose the correct corner less frequently than the control group. However, as seen in the right-hand panel of Figure 1.4, this prediction does not follow from the model. The figure shows the predicted probability of heading directly for the correct corner after being released into the triangle in the absence of any landmarks, after increasing amounts of training for the overshadowing and blocking groups. There is very little difference throughout training between the two groups. This pattern of results is predicted because the common cue (B) will restrict gains in associative strength to G_C in both groups. However, this overshadowing influence will be greater in the control group (see left-hand panel of Figure 1.4) because the landmark will overshadow B as well as G_C in the overshadowing group. Given the nature of Equation 1.3, the denominator will thus be greater in the control group than the overshadowing group and result in the probability of approaching the correct corner being approximately the same for both groups. The worked example below shows how Equation 1.3 is implemented and leads to the probability of choosing the correct corner on a test trial being approximately the same between the groups for the overshadowing example just

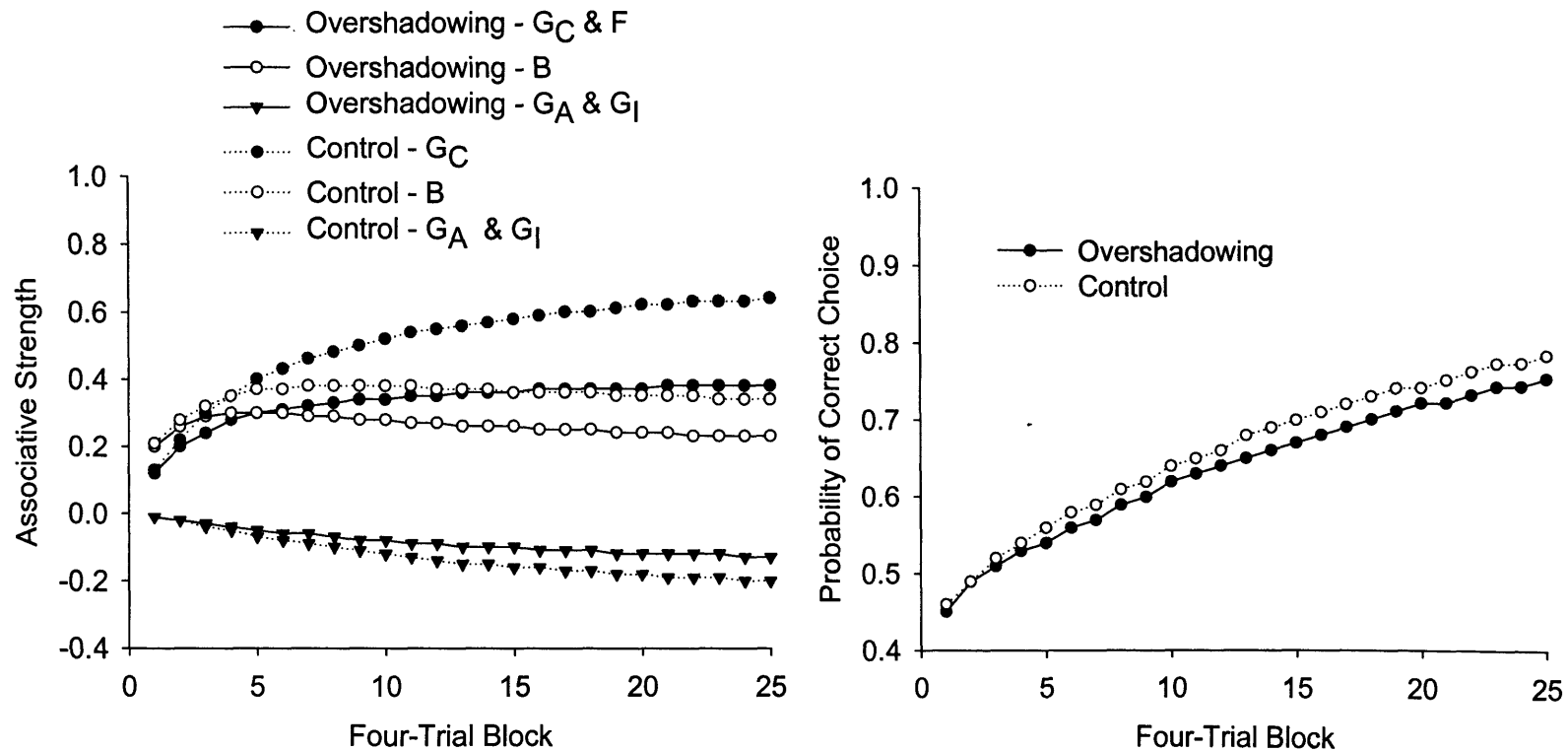


Figure 1.4. The results from computer simulations of the overshadowing experiment shown in the first row of Figure 1.1 based on the associative model of geometry learning by Miller and Shettleworth (2007). Left-hand panel: The predicted acquisition of associative strength by all of the cues in the triangular arena for the overshadowing, and control groups. Right-hand panel: The predicted probability of heading directly for the correct corner after being placed in the triangle arena in the absence of any landmarks, and after increasing amounts of training, for the overshadowing and control groups. G_C , G_I , G_A = the geometric cues at the correct corner, incorrect corner and apex respectively. F = the landmark, B = the common cue.

described after 100 trials of training. P_C is the probability of choosing the correct corner, V_C , V_I , and V_A represent to total associative strength of all the elements at the correct corner, incorrect corner and the apex respectively. G_C , G_I , and G_A , represent the associative strengths of the geometric cues at the correct and incorrect corners and the apex respectively. B represents the associative strength of the common cue.

$$P_C = \frac{V_C}{V_C + V_I + V_A} \quad (\text{Worked Example})$$

$$P_C = \frac{G_C + B}{(G_C + B) + (G_I + B) + (G_A + B)}$$

Overshadowing Group

$$P_C = \frac{.38 + .23}{(.38 + .23) + (-.13 + .23) + (-.13 + .23)}$$

$$P_C = \frac{.61}{.81}$$

$$P_C = .75$$

Control Group

$$P_C = \frac{.64 + .34}{(.64 + .34) + (-.2 + .34) + (-.2 + .34)}$$

$$P_C = \frac{.98}{1.26}$$

$$P_C = .78$$

1.5.2. Failure to Find Blocking of Geometric Cues-Miller & Shettleworth (2007)

The second and third rows of Figure 1.3 show a simple blocking design in the swimming pool. During Stage 1, the blocking group receives training with the platform randomly positioned in a circular pool with a landmark always attached to it. The control group does not receive Stage-1 training. After the completion of Stage 1, both groups receive identical training during Stage 2 in which they must locate the platform in one of the corners at the base of the triangular-shaped pool, in the presence of the landmark. Miller and Shettleworth (2007) assumed that for the blocking group, the landmark has an associative strength of 0.3 at the outset of Stage 2 because of the pre-training with the landmark during

Stage 1. The following simulations incorporate the same assumptions as Miller and Shettleworth.

The left-hand panel of Figure 1.5 shows the cumulative associative strength of each element for both groups as training in the triangle progresses. The same interpretation as to why there is a failure to observe overshadowing can be applied to the failure to observe blocking. The presence of the common cue (B) restricts gains in associative strength to G_C to a greater extent in the control group, than the blocking group because the landmark in this group also overshadows learning about B as well as G_C . It then follows that the denominator of Equation 1.3 will be greater in the control than in the blocking groups and will result in the probability of choosing the correct corner in the absence of the landmark being approximately the same for both groups. The right-hand panel of Figure 1.5 confirms this prediction by showing the probability of choosing the correct corner in the absence of any landmarks across successive trials. Even though there is a slight blocking effect, Miller and Shettleworth presumably assumed this difference would be too small to detect.

1.5.3. Potentiation of Geometric Cues-Miller & Shettleworth (2007).

The bottom row of Figure 1.3 shows a simple potentiation design. Both groups are trained in a kite-shaped pool with the platform always located in one of the right-angled corners. For the potentiation group the correct corner is formed by two adjacent white walls, while the opposite corner is formed by two adjacent black walls. A test trial is conducted in an all white kite in the absence of the platform. Miller and Shettleworth (2007) assume that each corner has a distinct featural element. They also assume that the colour at the incorrect corner (F_I) has an initial associative strength of 0.3 and a salience of 0.08, compared to 0.04 for the remaining cues. This is to take into consideration the report by Graham et al. (2006) that the black corner appears to be innately attractive, with rats approaching this corner

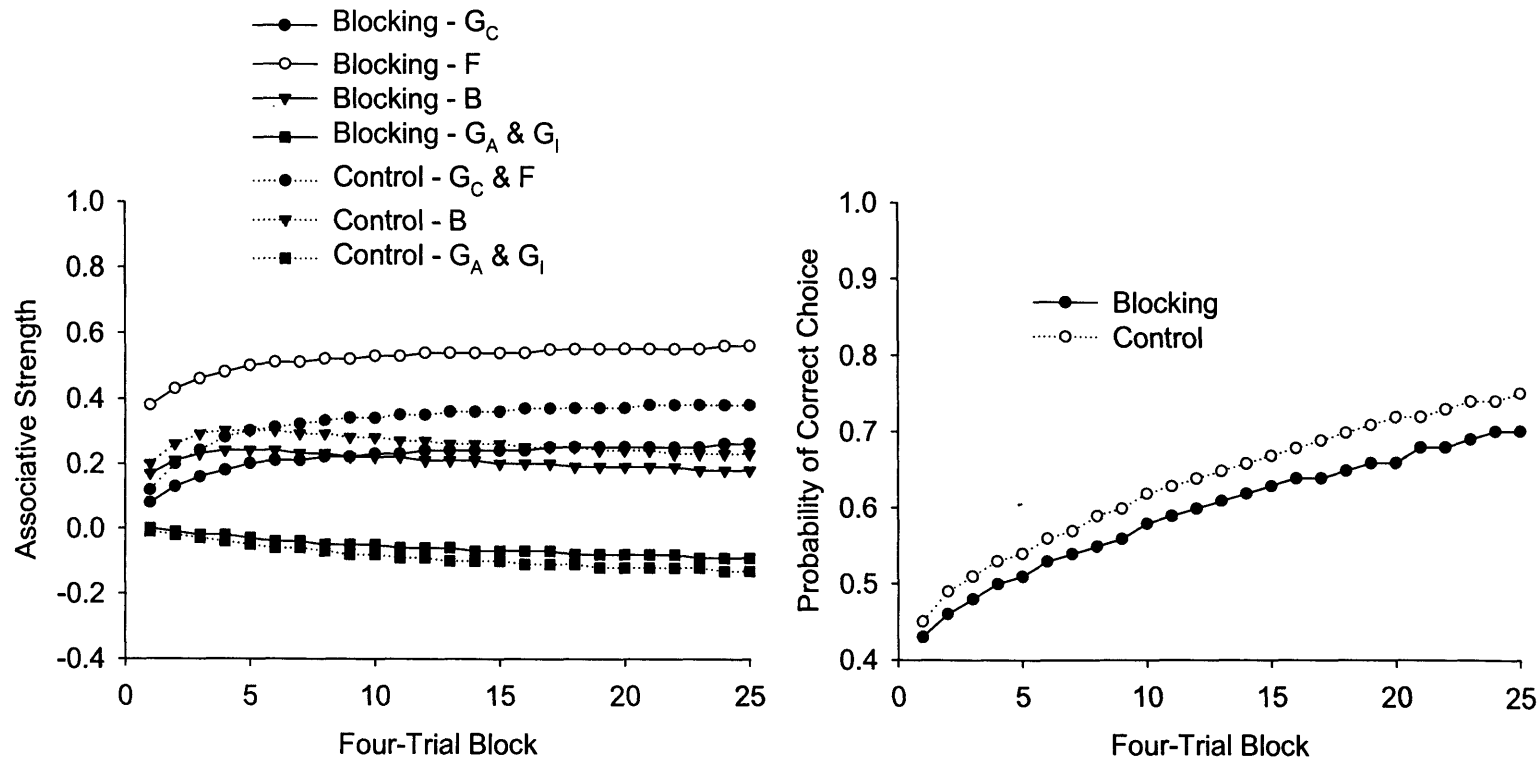


Figure 1.5. The results from computer simulations of the blocking experiment shown in the second and third row of Figure 1.1 based on the associative model of geometry learning by Miller and Shettleworth (2007). Left-hand panel: The predicted acquisition of associative strength by all of the cues in the triangular arena for the blocking and control groups. Right-hand panel: The predicted probability of heading directly for the correct corner after being placed in the triangle arena in the absence of any landmarks, and after increasing amounts of training, for the overshadowing and control groups. G_C , G_I , G_A , = the geometric cues at the correct corner, incorrect corner and apex respectively. F = the landmark, B = the common cue.

significantly more often than the remaining corners, even on the first trial. This initial associative strength and higher salience of the colour of the incorrect corner is important because it enables their model to successfully predict potentiation. On the first few trials of training rats will choose the incorrect corner more often than chance due to the higher salience and initial associative strength of the coloured walls. Since the platform is not located in this corner, the elements at that corner will lose associative strength. In particular, the geometric cue at the incorrect corner (G_1) will become inhibitory more quickly than in the control group. Thus on test trials in the absence of colour and the platform, rats in the potentiation group are likely to spend more time in the correct quadrant of the pool than the control group by virtue of avoiding the inhibitory incorrect corner to a greater extent.

1.5.4. Limitations of Miller and Shettleworth's (2007) Model

As a general note about Miller and Shettleworth's (2007) associative model, predictions from it are very parameter dependant. Slight changes in salience or associative strength may make the difference of whether or not cue competition takes place. Miller and Shettleworth take advantage of this flexibility with their analyses of blocking and potentiation. For example, their interpretation for the failures to find blocking of geometric cues by a landmark depends on the assumption that the landmark, during the initial stage of the experiment, only acquires a small amount of associative strength ($V_F = 0.3$). Why they predict such a low amount of associative strength is unclear, but if the associative strength of the landmark is greater at the outset of the second stage, the model predicts blocking will be observed. One way to achieve this outcome is to increase the length of pre-training with the landmark. An extended pre-training stage may endow the landmark with sufficient associative strength to act as a blocking cue in the subsequent stage (see Chapter 3).

Another assumption concerns potentiation. The salience of the featural element of the incorrect corner in the example provided in Figure 1.1, was set at a higher value ($\alpha = 0.08$) than the other cues ($\alpha = 0.04$) and also had an initial associative strength greater than 0 ($V_F = 0.3$). As noted above, they justified this assumption by referring to the study by Graham et al. (2006). However, it follows from their analysis that constructing the correct corner from two black walls and the opposite corner from two white walls will result in the geometric cues being overshadowed rather than potentiated. Graham et al. (2006) conducted this experiment and still found a significant, yet smaller, potentiation effect. This result challenges Miller and Shettleworth's (2007) interpretation of potentiation and thus an alternative explanation is worth investigating (See Chapters 5 and 6).

A second and more general problem with Miller and Shettleworth's (2007) model, which it shares with the Rescorla-Wagner (1972) theory, is the problem with attention. In both overshadowing and blocking paradigms a selective attention mechanism may be at work (e.g., Sutherland & Mackintosh, 1971). In a blocking design, the initial pre-training phase with the landmark may result in the animal paying all of its attention to the landmark. It then follows that during the second stage, where the landmark and the geometric cues are both present, the animal will continue to pay attention to the landmark and fail to attend to the geometric cues. This will then result in little learning about the significance of the geometric cues. A similar explanation of overshadowing can be used if one assumes the salience of the landmark to be greater than the geometric cues. An animal may focus all of its attention on the landmark and fail to notice the geometric cues. This will result in the landmark overshadowing learning about geometric cues. It is difficult to avoid this confound of interpretations when using an overshadowing and blocking paradigm. The ambiguity surrounding the interpretation of their results does, however, question whether we should reconsider the use of overshadowing and blocking designs to test whether spatial cues

interact in a way that is predicted by associative theories that are governed by a competitive learning rule (see Chapter 4).

1.6. Organisation and Rationale for Thesis

The failure to find overshadowing and blocking in environments with a distinctive shape in the past has been taken as evidence that the principles of associative learning do not extend to spatial learning. We have seen that the model of Miller and Shettleworth (2007) is good at explaining some of the results from past studies, but their model needs further evaluation. The overall purpose of this thesis is to provide this evaluation.

The introduction of Miller and Shettleworth's (2007) associative model of learning in environments with a distinctive shape provided an elegant way of interpreting the past failures to find overshadowing and blocking within an associative framework. Chapters 2 and 3 attempt to evaluate further this model by examining if overshadowing and blocking of geometric cues can be found with procedures which, according to Miller and Shettleworth (2007), should be successful in producing these effects.

Even if overshadowing and blocking are found, these effects would not unequivocally support the notion that the interaction between geometric and non-geometric cues is governed by the principles of associative learning, because of the attentional problem previously described. The experiments in Chapter 4 were designed in order to test the proposals of Miller and Shettleworth (2007) in such a way that a confirmation of predictions from the model could not be explained in terms of animals paying more attention to one stimulus than another.

Lastly, questions in this chapter were raised about the account offered by Miller and Shettleworth (2007) for potentiation. Chapters 5 and 6 look in more detail at this explanation.

Chapter 2: The effect of geometric salience on overshadowing in an environment with a distinctive shape

2.1. Introduction

As was discussed in the general introduction, when geometric cues and a landmark provide redundant information regarding the location of a goal, the individual landmarks consistently have failed to overshadow learning about geometric cues (Hayward et al., 2003; Hayward et al., 2004; Kelly et al., 1998; Pearce et al., 2001). However, Miller and Shettleworth's (2007) associative model of learning about geometric cues appears to reconcile these instances of failing to find overshadowing of geometric cues within an associative framework. The aim of this chapter is evaluate Miller and Shettleworth model of learning about geometric cues using an overshadowing design in which they clearly predict overshadowing to occur. Such a design has already been used in Pearce et al. (2001).

Pearce et al. (2001; Experiment 4) trained two groups of rats in a triangular pool. In an overshadowing group, a platform and landmark was located in one corner at the base of the triangle. A two-landmark control group received the same training except an identical landmark was also located in the opposite corner (see Figure 2.1). Miller and Shettleworth (2007) did not simulate this experiment. Given the nature of the two-landmark control condition, when rats choose the correct corner during training, the landmark would be expected to gain associative strength. However, in subsequent trials, the presence of the second landmark for the control group will encourage rats to approach the incorrect corner to a greater extent than the experimental group, which will have two consequences. First, choices to the incorrect corner will reduce the associative strength of the landmark and disrupt overshadowing and second, choices to the incorrect corner will result in the geometric cues at the incorrect corner gaining greater negative associative strength than for the overshadowing group. During test, the two-landmark control group will then be

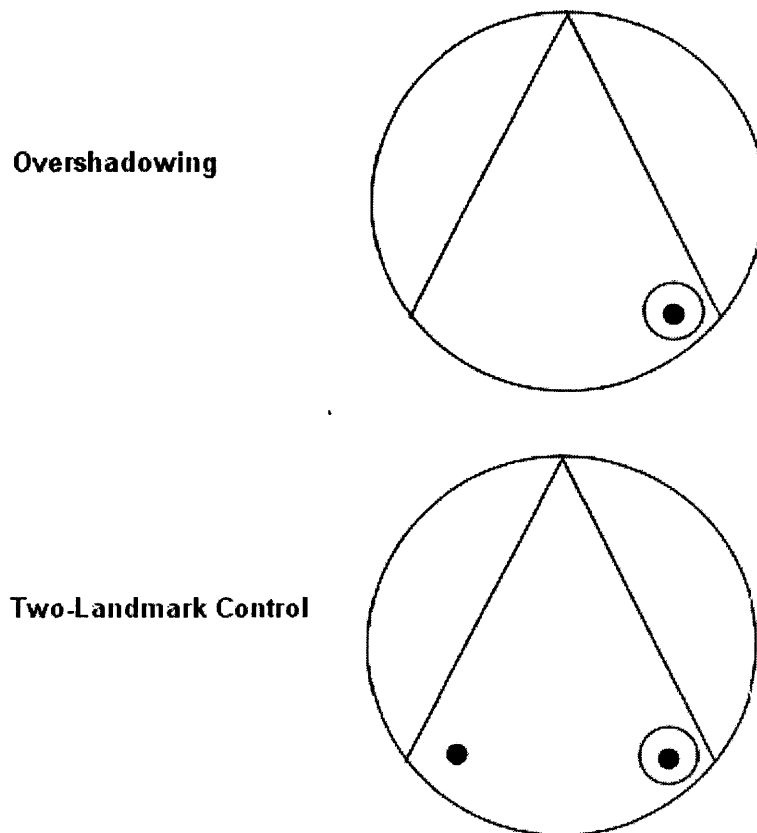


Figure 2.1. Schematic representation of the training conditions for the overshadowing and two-landmark control groups in Experiment 4 of Pearce et al. (2001). The small white circle represents the platform and the black circle represents the landmark.

expected to be more likely to choose the correct corner with a higher probability than the overshadowing group and thus result in overshadowing. In fact this is what is predicted by Miller and Shettleworth's model. The left-hand panel of Figure 2.2 shows the associative strengths of the geometric cues at the correct (G_C), and incorrect (G_I) corners, and the landmark (F) for the overshadowing group and the two-landmark control group in the experiment just considered. The parameters for the simulation were the same as that laid out in Chapter 1 (see p. 35). The simulation revealed that the associative strength of G_C for the two-landmark control group increases faster than the overshadowing group. Also, the associative strength of G_I for the two-landmark control group becomes negative faster than for the overshadowing group. These associative strengths translate well during testing. The right-hand panel of Figure 2.2 shows the probability of choosing the correct corner in the absence of the platform and landmarks as training progresses. Clearly, the probability of choosing the correct corner is less in the overshadowing group than in the two-landmark control group and this difference increases as training progresses.

Given the two-landmark control group, it is clear that Miller and Shettleworth (2007) predict overshadowing. The purpose of the reported experiments was to evaluate this prediction. Pearce et al. (2001) found no overshadowing even when the two-landmark control was used. Making strong conclusions based on a null result is not wise and for this reason it was necessary to replicate Pearce et al. experiment to confirm the reliability of this result. In order to confirm its generality a black, spherical landmark hanging above the pool rather than a landmark attached to the platform was used.

2.2. Experiment 1

Two groups of rats were trained in a triangular-shaped pool. An overshadowing group was trained with the platform located at one of the corners at the base of the triangle with

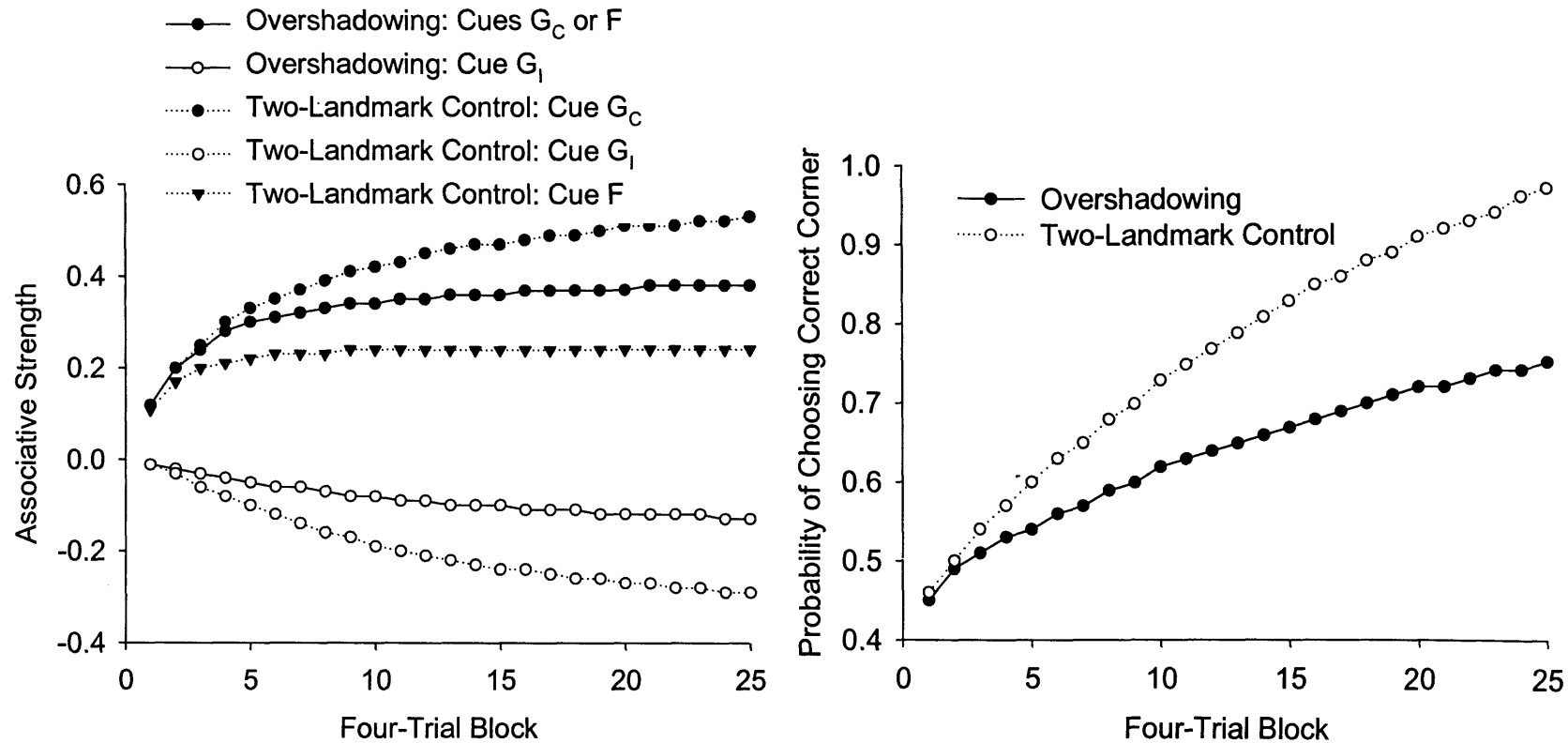


Figure 2.2. The results from computer simulations of an overshadowing experiment with an overshadowing and two-landmark control group based on the associative model of geometry learning by Miller and Shettleworth (2007). Left-hand panel: The predicted acquisition of associative strength by all of the cues, except the common cue, B, in the triangular arena for the overshadowing, and two-landmark control groups. Right-hand panel: The predicted probability of heading directly for the correct corner after being placed in the triangle arena in the absence of any landmarks, and after increasing amounts of training, for the overshadowing and two-landmark control groups. G_C , G_I , G_A = the geometric cues at the correct corner, incorrect corner and apex respectively. F = the landmark.

a spherical landmark located directly above the platform. The control group received identical training, but received another identical landmark positioned in the opposite corner. Upon completion of 12 sessions, both groups were tested in the triangular-shaped pool with the platform and landmarks removed. If the predictions based on Miller and Shettleworth (2007) are correct, then during this test the overshadowing group will spend less time searching in the zone where the platform had been located during training than the control group. Since this was found to be incorrect, and because Miller and Shettleworth also predict that overshadowing increases with extended training, an additional 12 sessions of training were completed and the groups were tested again in the same manner as the previous test trial.

2.2.1. Method

Subjects. Twenty, naïve, male, hooded Lister rats (*Rattus norvegicus*), obtained from Harlan Olac (Bicester, Oxon, England), and weighing between 250 g – 300 g at the start of the experiment were used. Rats were housed in white plastic cages with secured metal grid lids and maintained on a 12-hr/12-hr light/dark cycle with lights on at 0700. Subjects were housed in pairs and had continuous access to food and water in their home cages.

Apparatus. A white, circular pool measuring 2 m in diameter and 0.6 m deep was used. The pool was mounted on a platform 0.6 m from the floor in the middle of the room (4 m X 4 m X 2.3 m). The pool was filled with water to a depth of 27 cm and was maintained at a temperature of 25°C ($\pm 2^\circ\text{C}$). To make the water opaque, 0.5 L of white opacifer E308 (Roehm and Haas, U.K., Ltd., Dewsbury) was used. The water was changed daily.

A white circular ceiling, measuring 2 m in diameter, was suspended 1.75 m above the floor of the pool. In the centre of the ceiling was a hole measuring 30 cm in diameter in which a video camera with a wide-angled lens was situated. The lens of the camera was 25

cm above the hole and was connected to a video monitor and computer equipment in an adjacent room. During tests, the rats' movements were analyzed using Watermaze software (Morris & Spooner, 1990). The pool was illuminated by eight 45-W lights that were located in the circular ceiling above the pool. The lights were 22.5 cm in diameter and were equidistant from each other in a 1.6 m diameter circle whose centre was coincident with the centre of the circular ceiling. A platform measuring 10 cm in diameter and mounted on a column was used during all training trials. The surface of the platform had a series of concentric ridges. The base of the column rested on the bottom of the pool and the platform surface was 2 cm below the surface of the water. A white curtain was drawn around the pool during all training and test trials. The curtain, which was attached to the edge of the circular ceiling, was 1.5 m high and fell 25 cm below the edge of the pool. A black spherical landmark, 8 cm in diameter was used. The landmark was attached to a clear Perspex rod that could be attached to the walls creating the shape of the pool. The lowest point of the landmark was 33 cm above the surface of the water.

The training room was additionally lit by two 1.53-m strip lights connected end to end on each of the East and West walls. These lights ran parallel with the floor and were situated 75 cm above the floor. There was a door (1.75 m X 2 m) in the centre of the South wall. To create the triangular-shaped pool, two, white, Perspex boards (1.8 m long, 0.59 m high, and 2 mm thick) were placed vertically in the pool and suspended by bars that extended over the edge of the pool.

Procedure. The experiment consisted of 24 sessions of training. Rats completed one session of training each day. Each session contained 4 trials. Rats were carried into a room adjacent to the test room in groups of five in a light-tight box. They remained in this box between trials. Each rat was carried from the box to the pool and was released facing the centre of a wall. The release point varied across trials with the stipulation that each wall was

used once in any given session and one release point was used twice. The release point that was used twice varied between sessions such that over three sessions, each release point was used four times. During a trial, the rat was required to swim to a submerged platform. Each trial lasted a maximum of 60 s. If the rat did not find the platform within 60 s, the experimenter guided it to the platform. After climbing on the platform the rat remained there for 20 s before being lifted from the pool, dried and returned to its holding container. The inter-trial interval for each rat was approximately 5 min. Between each trial, the experimenter rotated the arena 90°, 180°, or 270° clockwise. Four possible orientations were used (North, South, East or West). The orientation of the triangular arena across trials varied randomly with the only stipulation being that each orientation was used once for any given session.

Rats were randomly assigned to two groups in equal number ($n = 10$): an overshadowing group and a control group. During training, for the overshadowing group the platform was 25 cm from one of the corners at the base of the triangle on an imaginary line that bisected the corner. On all trials a spherical landmark was located directly above the platform. The platform was in the corner where the long wall was to the left of the curved wall for half of the rats and the opposite corner for the remaining rats. The control group received the same training except another, identical, landmark was located in the opposite corner at the base of the triangle 25 cm from the corner on an imaginary line that bisected the corner. The first three trials of Sessions 12 and 24 were conducted in the same manner as described previously. The fourth trial of these sessions was a geometry test. During these test trials, the platform and landmarks were removed from the pool. The rats were placed in the centre of the arena and allowed to swim for 60 s.

Throughout the experiment, except for the test trial, a record was taken of whether, after being released, a rat entered first the correct corner of the pool – the corner containing

the platform. A rat was deemed to have entered any of the three corners if its snout crossed a notional circular line with a radius of 40 cm and with its centre at the point where the walls creating the corner met. For ease of exposition, the term correct choice will be used to refer to those occasions when a rat entered the correct corner before any other corner. Also, as an additional measure of performance, latencies to find the platform were recorded. For the purpose of analysing the results from the test trials, circular search zones were used. Each search zone had a diameter of 30 cm with its centre positioned 25 cm from a corner on a line that bisected the corner. The percentage of time spent in the correct (the one where the platform had been located) and incorrect (the symmetrically opposite corner) zones of the triangular-shaped pool were analyzed. A Type-1 error rate of 0.05 was adopted for all reported statistical comparisons.

2.2.2. Results and Discussion

The left-hand panel of Figure 2.3 shows the mean latencies to find the hidden platform across the 24 sessions of the experiment. Both groups became faster at finding the platform as training progressed. The control group was slightly slower than the overshadowing group at finding the platform in the first half of training, but by the end of training there was no apparent difference between the groups. A t-test was conducted on the individual mean latencies of the first three sessions combined and revealed a significant difference between the groups, $t(18) = 5.37$. An identical analysis was conducted on the last three sessions combined and revealed no differences between the groups, $t(18) = 0.31$.

The right-hand panel of Figure 2.3 shows the percentage of correct choices during the 24 training sessions. Both groups started poorly and quickly improved their performance across training. By the end of training, both groups were making correct choices on virtually every trial. A Mann-Whitney U test was conducted on the individual mean percentage of

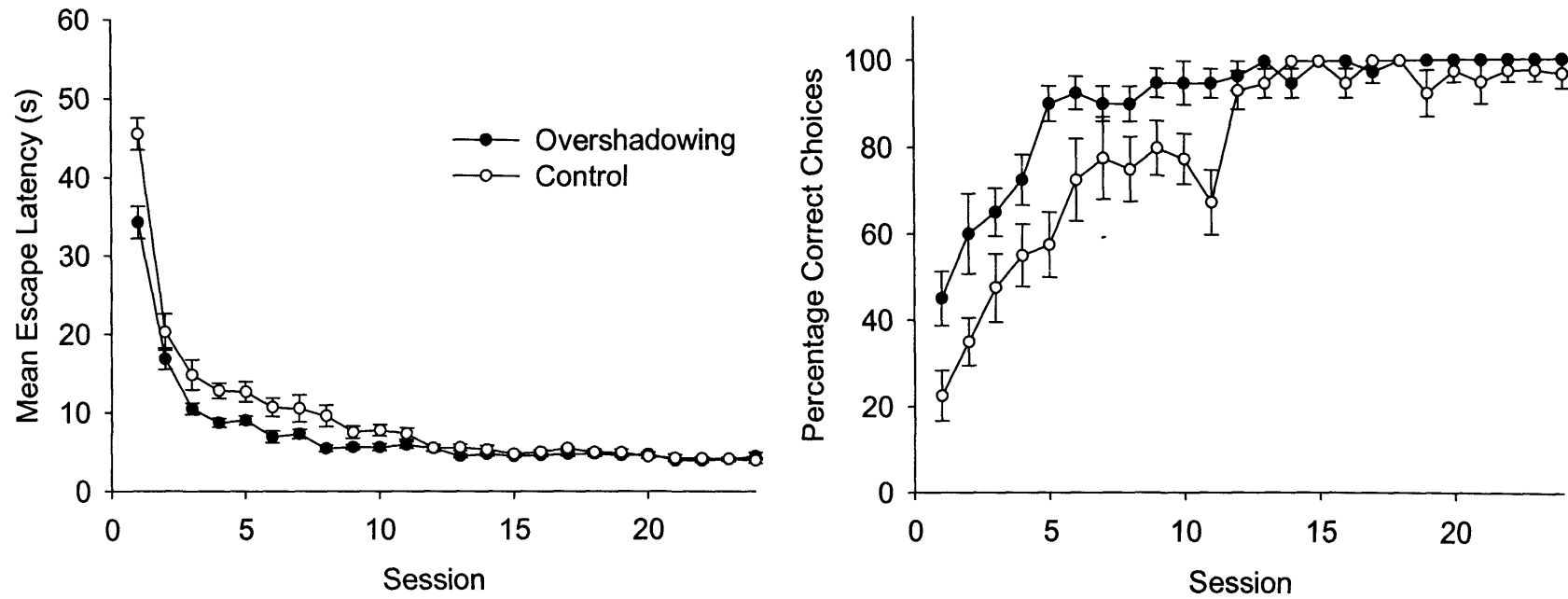


Figure 2.3. Mean (+SEM) escape latencies (left-hand panel) and mean (+SEM) percentage of correct choices (right-hand panel) for the overshadowing and control groups of Experiment 1.

correct choices for first three sessions combined revealed a significant difference between the groups, $U(10, 10) = 6.5$. An identical analysis on the last three sessions combined revealed no difference between the groups, $U(10, 10) = 40.0$. The initial difference between the overshadowing and control groups on latencies and choices establishes that the landmark present in the overshadowing group did in fact have an effect on performance, and the rats are simply not ignoring the landmark.

Figure 2.4 shows the time spent in the correct and incorrect zones during the geometry test trials on Sessions 12 (left-hand panel) and 24 (right-hand panel). Both test trials revealed the same pattern of findings except rats showed greater responding during the test trial conducted on Session 24. Although both groups spent more time in the correct than the incorrect zone, both groups spent approximately equal time in the correct zone. A 2 X 2 X 2 (Group X Zone X Test) ANOVA was conducted. The analyses revealed a significant main effect of zone, $F(1, 18) = 122.87$, test, $F(1, 18) = 11.02$, and a significant Zone X Test interaction, $F(1, 18) = 14.79$. The remaining findings from the ANOVA were not significant, $F_s < 1$. Simple effects analysis on the Zone X Test interaction revealed that on both tests, both groups spent a greater proportion of time in the correct than the incorrect zone, $F_s(1, 36) > 43.40$ and time spent in the correct zone on Test 2 was greater than in Test 1, $F(1, 36) = 25.80$. However, time spent in the incorrect zone did not differ across tests, $F < 1$.

The results from the two test trials revealed identical findings from the overshadowing and control groups. It is clear from the results that a landmark above the platform did not restrict at all learning about geometric cues when compared to a group that received two landmarks in the pool. The general increase in time spent in the correct zone in Test 2 from Test 1 confirms the beneficial effect of extended training. However, extended training did not result in overshadowing. These results replicate previous results by Pearce et al. (2001)

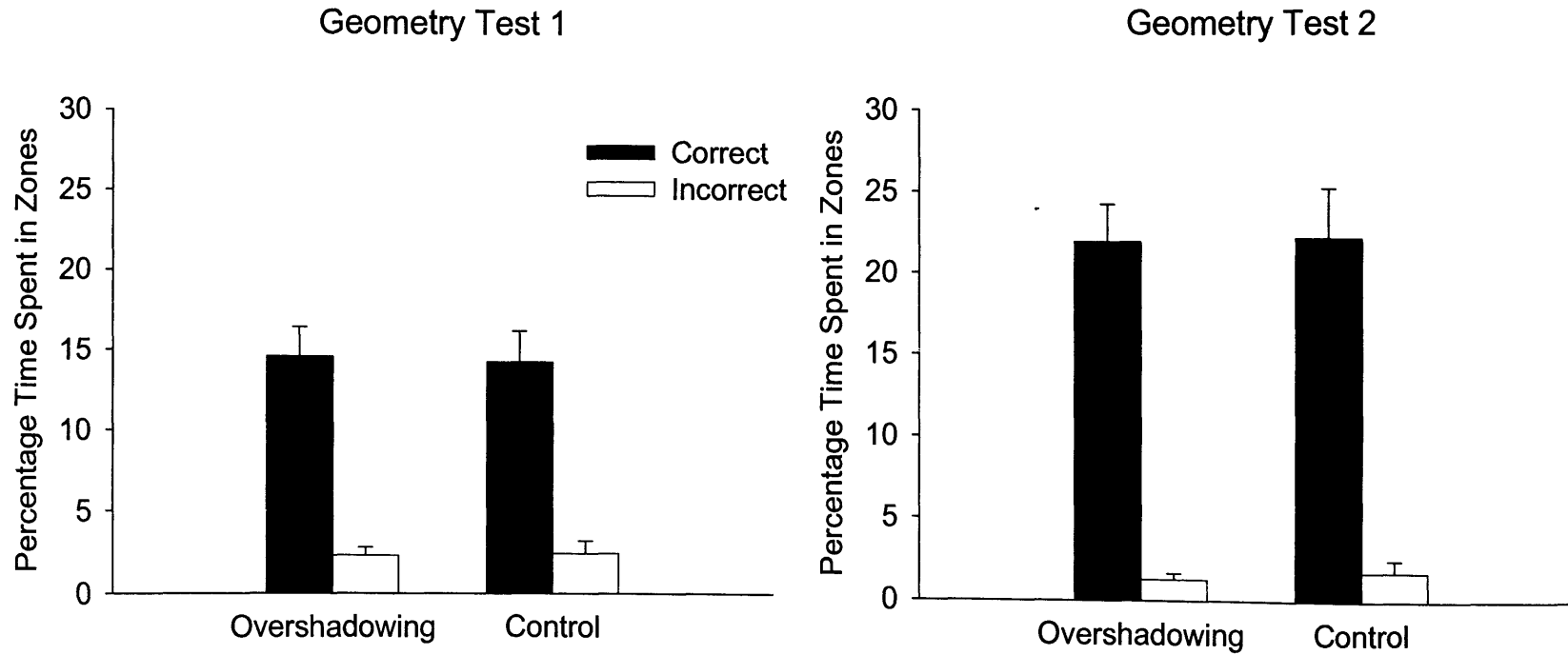


Figure 2.4. Mean (+SEM) percentage of time spent in the correct and incorrect zones during the geometric test trials on Session 12 (left-hand panel) and on Session 24 (Right-hand panel).

and imply that the model of Miller and Shettleworth (2007) does not provide a complete account of learning about geometric cues.

2.3. Experiment 2

Experiment 1 demonstrated that a landmark failed to overshadow learning about geometric cues even though the model of Miller and Shettleworth (2007) predicted overshadowing should occur. The model of Miller and Shettleworth predicts that the extent of overshadowing between geometric cues and a landmark will be governed by their relative salience. It is thus possible that the results of Experiment 1 can be resolved using their model. For instance, if in Experiment 1, the geometric cues of the environment were more salient than the landmark, overshadowing geometric cues would be difficult. This prediction follows from the theory of Miller and Shettleworth. A simulation was conducted, based on the design of Experiment 1, where the salience of the landmark was reduced to 0.01 and the salience of the geometric cues and common cue was 0.04. The left-hand panel of Figure 2.5 shows the probability of choosing the correct location in the absence of the platform and landmark across training. Compared to the left-hand panel of Figure 2.2, the extent of overshadowing is markedly reduced when the salience of the landmark is less than that of the geometric cues. Thus in order to increase the chance of observing overshadowing, the salience of the landmark would need to be greater relative to the salience of the geometric cues. This can be accomplished by either increasing the salience of the landmark or decreasing the salience of the geometric cues. It is possible that increasing the size of the landmark will increase its salience, but pilot work in the laboratory suggested that increasing the size of the landmark has no impact on its influence on behaviour. For instance, a 1-m tall cylindrical column, located near the platform did not overshadow learning about geometric cues in a rectangular arena. Thus altering the salience of the geometric cues was attempted.

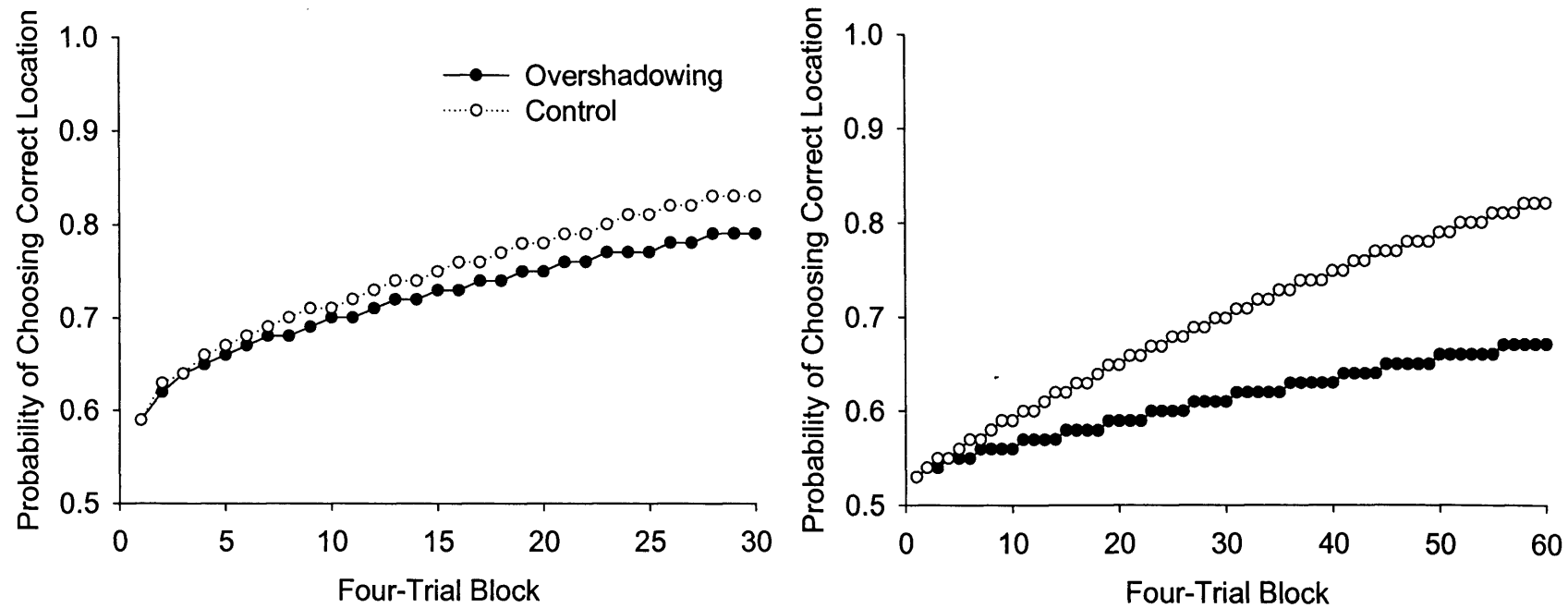


Figure 2.5. The left-hand panel shows the probability of choosing the correct location in the absence of any landmarks over the course of training. This simulation was based on the associative model of geometry learning by Miller and Shettleworth (2007) where the salience of the landmark was 0.01 and the salience of the remaining cues was 0.04. The right-hand panel shows the same simulation except the salience of the geometric cues was 0.01 and the salience of the remaining cues was 0.04. Only two choice locations were used for these simulations.

To decrease the salience of geometric cues, the platform was moved 60 cm away from the correct corner.

The model of Miller and Shettleworth (2007) also predicts that lowering the salience of the geometric cues will result in overshadowing occurring more readily. To confirm this prediction a simulation was conducted where the salience of the geometric cues was 0.01 and the salience of the remaining cues was 0.04. The right-hand panel of Figure 2.5 shows the results from the simulation for an overshadowing and control group trained as their namesakes in Experiment 1. It can clearly be seen that when the geometric cues have lower salience, the difference between the overshadowing and control groups is larger than when the salience of geometric cues is higher than the landmark (see left-hand panel of Figure 2.5). Given this prediction, before looking at overshadowing, Experiment 2 was conducted in order to confirm that by moving the platform some distance from the corner does indeed reduce the salience of geometric cues. Only two choice locations were used in the analysis of the results from the experiment; one where the platform was located, and another in the symmetrically opposite location. To take this into consideration the simulations shown in Figure 2.5 were conducted with only two choice locations.

Two groups of rats were trained in a triangular-shaped pool. The platform was placed in one of two areas of the pool, depending upon the group. A high salience groups was trained with the platform in a corner in the same manner as for the previous experiment. A low salience group was trained with the platform moved 60 cm away from the corner along the straight wall, at a distance of 18 cm from this wall. By moving the platform some distance from the corner, it was intended to reduce the salience of the geometric cues. Acquisition of this task was measured through periodical test trials with the platform removed from the pool. Time spent in the correct zone (the area where the platform had been located) was analyzed across multiple test trials. If moving the platform away from the corner

reduces the salience of geometric cues then during the test trials the low salience group should spend less time in the correct search zone than the high salience group

2.3.1. Method

Subjects and Apparatus. The 24 naïve rats were from the same stock, of approximately the same weight, and housed in the same manner as in Experiment 1. All rats were previously used in an appetitive conditioning experiment for which they were reduced to 80% of their free-feeding weights. After the completion of this experiment the rats were allowed free access to food for two weeks before the start of Experiment 2. The apparatus was identical to that of Experiment 1 except no landmarks were used in this experiment.

Procedure. Rats were randomly assigned to two groups in equal numbers ($n = 12$): a high salience and a low salience group. During training, the high salience group received the platform 25 cm from one of the corners at the base of the triangle on an imaginary line that bisected the corner. The platform was located in the corner where the long wall was to the right of the curved wall for half the rats, and in the opposite corner for the remaining rats. For the low salience group, the platform was situated 60 cm along a long wall from one of the corners at the base of the triangle, and it was located 18 cm on an imaginary line perpendicular to the wall. For half of the rats the platform was 60 cm from the corner that was constructed from a long wall to the right of the curved wall, while for the other half the platform was 60 cm from corner constructed from a long wall to the left of the curved wall. Each rat was carried from the holding box to the pool and was released facing the centre of a wall if part of the high salience group or directly facing a corner if part of the low salience group. As in Experiment 1, the release point varied so over three sessions, each release point was used four times. The first three trials of Sessions 3, 6, 9, 12 and 15 were conducted in the same manner as previous trials. The fourth trial of these sessions was a geometry test.

During these test trials, the platform was removed from the pool. The rats were placed in the centre of the arena and allowed to swim for 60 sec.

As in Experiment 1, latencies to find the platform were recorded. Choices were not recorded for this experiment because choice locations would not be equivalent between the groups given their different treatments. For the purpose of analysing the results from the test trials, circular search zones, identical to those used in Experiment 1, were used. Each search zone had a diameter of 30 cm with its centre coincident with the centre of the where the platform was located. The percentage of time spent in the correct (the one where the platform had been located) and incorrect (the symmetrically opposite location) zones of the triangular-shaped pool were analyzed. Any procedural details omitted were identical to Experiment 1.

2.3.2. Result and Discussion

Figure 2.6 shows the mean latencies to find the submerged platform across sessions. Rats in each group required less time to find the platform as training progressed. A t-test based on the individual mean latencies across the 15 sessions combined revealed that the low salience group spent more time searching for the platform than the high salience group, $t(22) = 2.15$. The difference between the high and low salience groups indicates that the platform was more difficult to find when positioned some distance away from the corner rather than directly in the corner. This is one indication that moving the location of the platform away from the corner of the pool successfully altered the salience of the geometric cues.

Figure 2.7 shows the time spent in the correct zone across the five test trials. Both groups spent rather little time in the correct zone on the first test trial, but the time spent in the zone increased as testing occurred later on in training. It appears that the high salience group improved their performance of searching in the correct zone at a faster rate than the

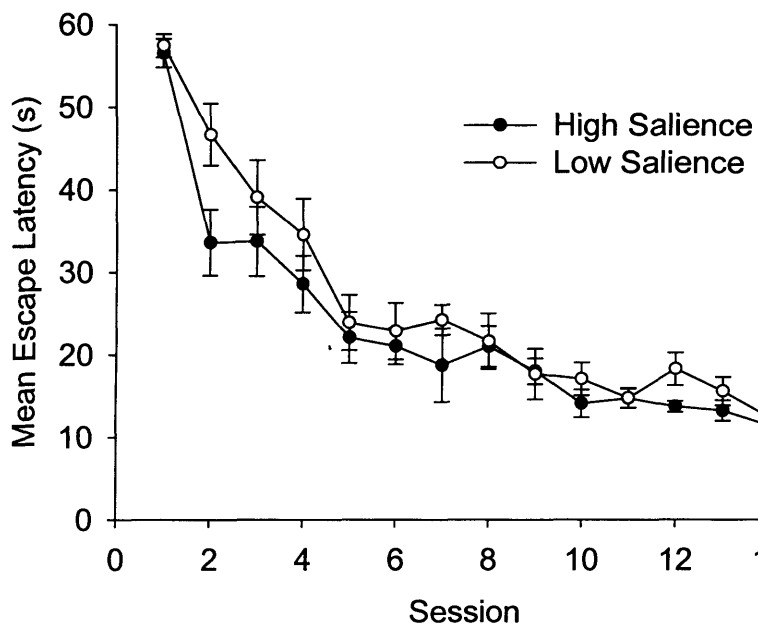


Figure 2.6. Mean (+SEM) time to find the submerged hidden platform for the high and low salience groups of Experiment 2.

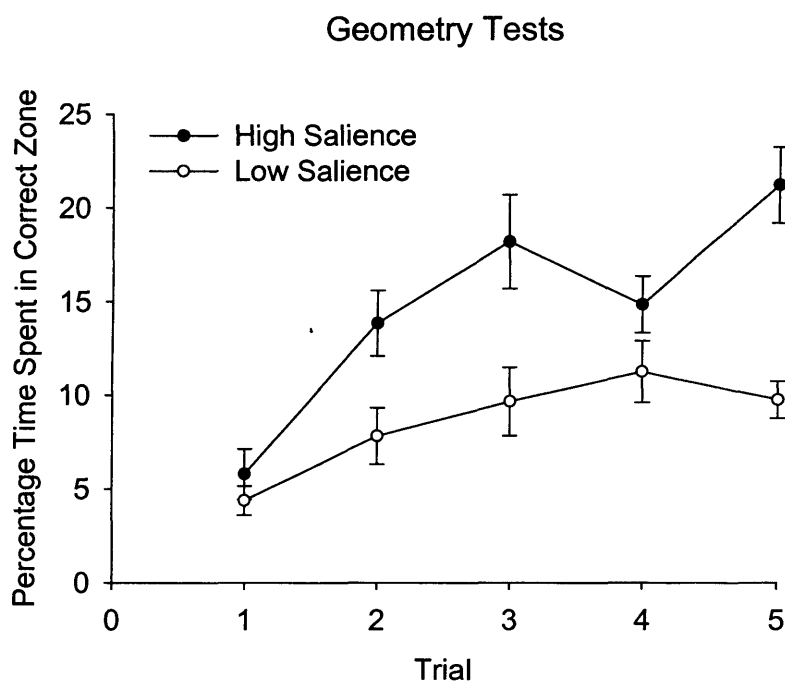


Figure 2.7. Mean (+SEM) percentage of time spent in the correct zone on multiple test trials conducted for the high and low salience groups of Experiment 2.

low salience group. This was confirmed by a 2 X 2 (Group X Session) ANOVA. The analysis revealed significant main effects of group, $F(1, 22) = 15.63$, session, $F(4, 88) = 17.36$, and a significant Group X Session interaction, $F(4, 88) = 4.17$. A simple effects analysis (Kirk, 1968) on the interaction revealed that both groups increased the time spent in the correct zone from the first to the last test trial, $F_s(4, 88) > 3.68$. More interestingly, on the second, third, and fifth test trial, the high salience group spent a significantly greater percentage of time in the correct zone than the low salience group, $F_s(1, 110) > 6.61$.

It is understandable that during the first test trial the two groups did not differ with respect to time spent in the correct zone. After only three sessions of training, not much learning about the significance of geometric cues appears to have taken place. The first test also ensured that the two groups did not differ with respect to any sort of unconditioned responding to the two locations. The differences between the group on Tests 2, 3 and 5 suggests that the high salience group learned the significance of the geometric cues in finding the location of the platform faster than the low salience group. As predicted, by moving the location of the platform from directly in the corner to some distance from the corner, the salience of the geometric cues was reduced successfully. The next logical step is to see if reducing the salience of geometric cues will result in overshadowing by a landmark situated above the platform. The next two experiments explored this possibility.

2.4. Experiment 3

An overshadowing group was trained with the platform 60 cm from one of the corners at the base of the triangle with a spherical landmark above it. A control group was given the same treatment except another identical landmark was positioned in the symmetrically opposite location in the pool.

As shown in the right-hand panel of Figure 2.5, if the salience of the geometric cues is low, relative to that of the landmark, then the theory of Miller and Shettleworth (2007) predicts that the former will be overshadowed by the latter. Moreover the magnitude of this effect is predicted to increase with extended training. Accordingly, test trials were given on Sessions 12, 18 and 24. If the salience of geometric cues is now lower or equal to the landmark, the overshadowing group should spend less time searching in the vicinity of the platform than the control group during a test trial and this difference should increase as training progresses.

2.4.1. Method

Subjects and Apparatus. The 18 rats were from the same stock, of approximately the same weight, and housed in the same manner as in Experiment 1. The apparatus was identical to that of Experiment 1.

Procedure. Rats were randomly assigned to two groups in equal numbers ($n = 9$): an overshadowing group and control group. Both groups were trained in a similar manner to that of the low salience group in the previous experiment except that both groups received a spherical landmark positioned directly above the platform. In addition, the control group had an additional, identical spherical landmark located in the symmetrically opposite location. In addition to latencies to find the platform, except for the test trials, a record was taken of whether, after being released, a rat entered first the correct zone (the zone that contained the platform) or incorrect zone (the symmetrically opposite zone) of the pool. Each zone was 30 cm in diameter and was positioned concentric with the centre of the platform location or where the platform would be located. Due to error, choices were not recorded for Session 1. Rats were trained for 24 sessions. The last trial on Sessions 12, 18 and 24 were geometry tests conducted in the same manner as in Experiment 1.

2.4.2. Results and Discussion

The left-hand panel of Figure 2.8 shows the latency to find the hidden platform across the 24 sessions of training. Both groups increased their speed at finding the platform and by the end of training both groups were taking the same amount of time to find the platform. A t-test was conducted on the individual mean latencies for the last three sessions combined confirmed the groups did not differ, $t(16) = 0.92$. An identical analysis was conducted on the first three sessions combined to determine if the landmark in the overshadowing group had an effect on performance. This analysis revealed a significant difference between the groups, $t(16) = 2.26$.

The right-hand panel of Figure 2.8 shows the mean percentage of correct choices for every training session except Session 1. By the end of training, both groups were making correct choices on the majority of trials, however, unlike with the latencies, the performance of the control group was inferior to that of the overshadowing group. An analysis on the individual mean correct choices for the last three sessions combined revealed a significant difference between the groups, $U(9, 9) = 15.5$. A similar difference was confirmed on the first three session, $U(9, 9) = 3.0$.

Figure 2.9 shows the mean percentages of time spent in the correct and incorrect zones for the three geometry tests conducted on Sessions 12, 18 and 24 respectively for both groups. In general, the results did not differ much across the three tests. Both groups spent more time in the correct zone than the incorrect zone, but time spent in the correct zone did not differ between the groups. A $2 \times 2 \times 3$ (Group \times Zone \times Test) ANOVA was conducted and revealed only a significant main effect of zone, $F(1, 30) = 106.43$ and test, $F(2, 32) = 4.33$. The remaining main effects and all the interactions were not significant, $F_s < 2.14$. Since there appears to be a hint of overshadowing in the final test conducted on Session 24, a separate 2×2 (Group \times Zone) ANOVA was conducted for this test. The analysis revealed a

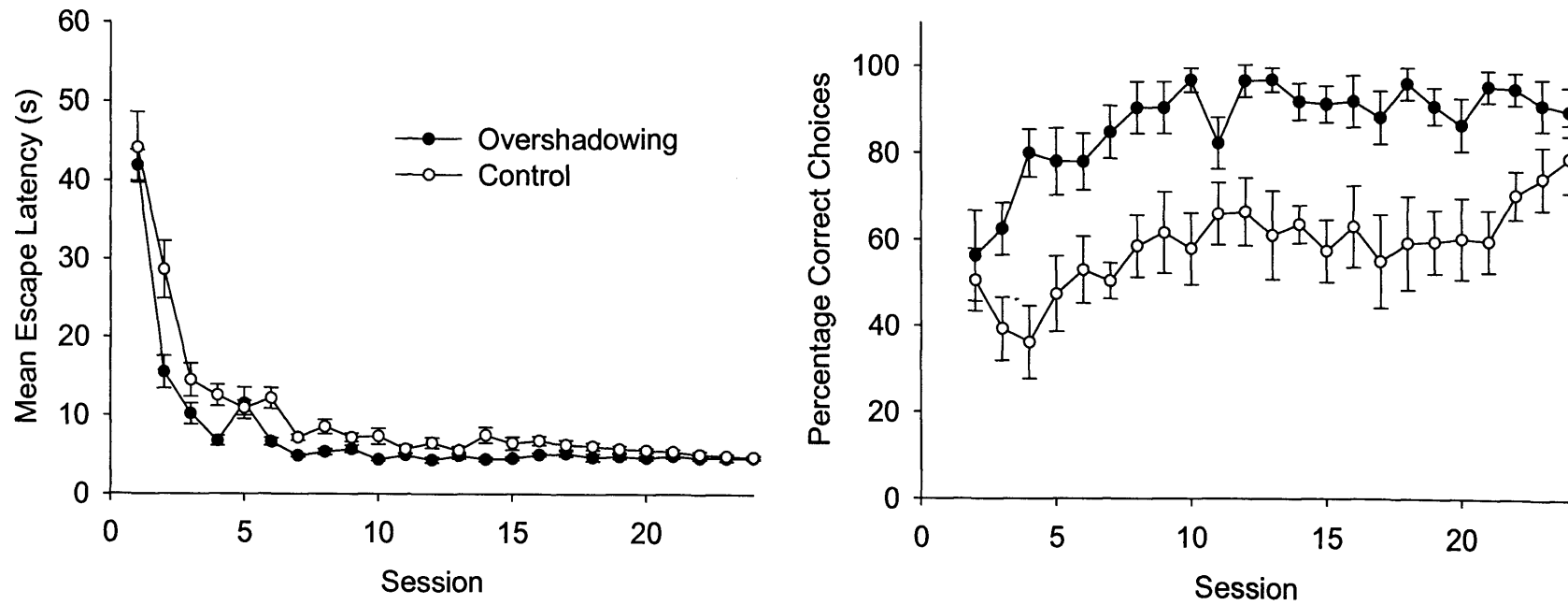


Figure 2.8. Mean (+SEM) escape latencies (left-hand panel) and mean (+SEM) percentage of correct choices (right-hand panel) for the overshadowing and control groups of Experiment 3.

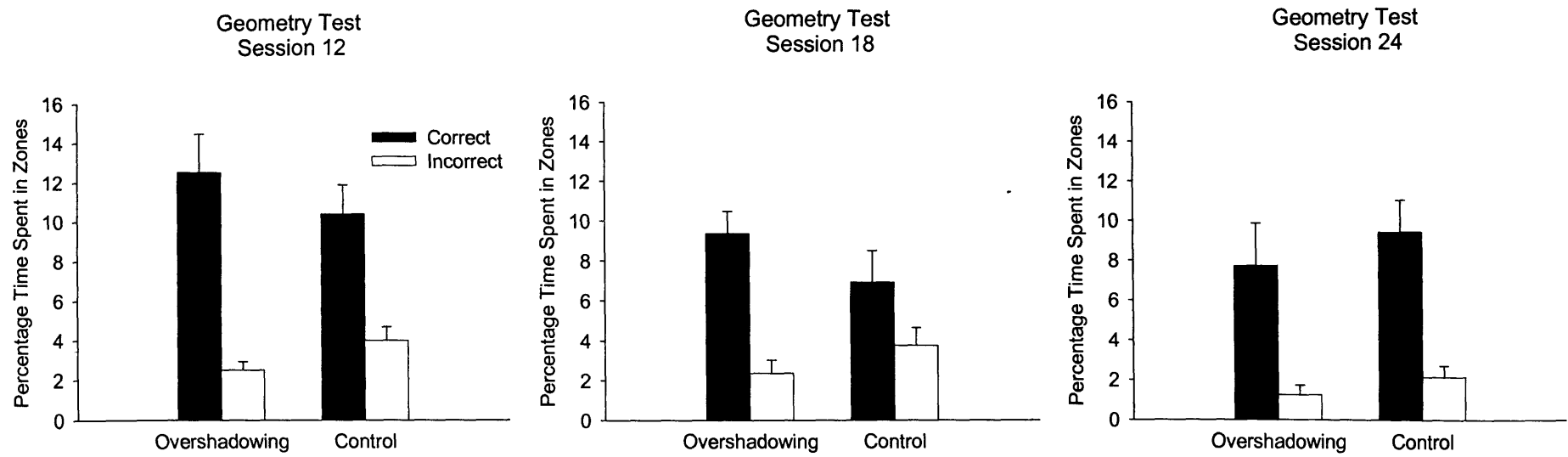


Figure 2.9. Mean (+SEM) percentage of time spent in the correct and incorrect zones for the overshadowing and control groups during the geometry test trials conducted on Sessions 12 (right-hand panel), 18 (centre panel), and 24 (right-hand panel) of Experiment 3.

significant zone effect, $F(1, 16) = 31.43$, but the main effect of group and the Group X Zone interaction were not significant $F_s < 1$.

The results clearly show that a landmark does not restrict at all learning about the location of the platform using geometric cues. Even when we tested late in training, no evidence of overshadowing was observed. It is possible that during the first test on Session 12, searching the pool in the absence of any landmarks resulted in reduced responding to geometric cues in subsequent tests in the absence of the landmark and therefore reduced our chances of observing overshadowing. In Experiment 4, only one test was conducted on Session 24 in order to maximise our chances of observing overshadowing.

2.5. Experiment 4

Experiment 4 was an exact replication of Experiment 3 except only one test trial was conducted on Session 24 in order to maximise the probability at observing overshadowing.

2.5.1. Method

Subjects and Apparatus. The 20 rats were from the same stock, of approximately the same weight, and housed in the same manner as in Experiment 1. 12 rats were previously used in an appetitive conditioning experiment, but had no experience in a swimming pool. The remaining rats were experimentally naïve. The apparatus was identical to that of Experiment 1.

Procedure. Rats were randomly assigned to two groups in equal numbers ($n = 10$): an overshadowing group and control group, with the only exception being that 4 naïve rats were allocated at random to each group. Both groups were trained as their namesakes in Experiment 3. All procedural details were identical to that of Experiment 3 except that only

one geometry test was conducted on the last trial on Session 24. The test was conducted in the same manner as in Experiment 1.

2.5.2. Results and Discussion

The left-hand panel of Figure 2.10 shows the latency to find the hidden platform across the 24 sessions of training. While both groups increased their speed at finding the platform the control group was consistently slower than the overshadowing group. A t-test, conducted on the individual mean latencies for the last three sessions combined, confirmed this difference, $t(18) = 5.99$. A similar result was found on the first three session, $t(18) = 2.89$.

The right-hand panel of Figure 2.10 shows the mean percentage of correct choices for each session of the experiment. By the end of training, both groups were making correct choices on the majority of trials, however, in contrast to the previous experiment, the control and overshadowing group showed no difference in the number of correct choices made by the end of training. This was confirmed with an analysis on the individual mean correct choices for the last three sessions combined, $U(10, 10) = 35.0$. However, an analysis on the first three session combined revealed a significant difference between the group, $U(10, 10) = 12.0$. This once again confirms that the landmark in the overshadowing group had an effect on performance.

Figure 2.11 shows the percentage of time spent in the correct and incorrect zones during the geometry test conducted on Session 24. Both groups spent more time in the correct zone than the incorrect zone, but time spent in the correct zone was virtually the same for both groups. A 2 X 2 (Group X Zone) ANOVA was conducted and revealed a significant main effect of zone, $F(1, 18) = 34.69$, but no main effect of group and no Group X Zone interaction, $F_s < 1$.

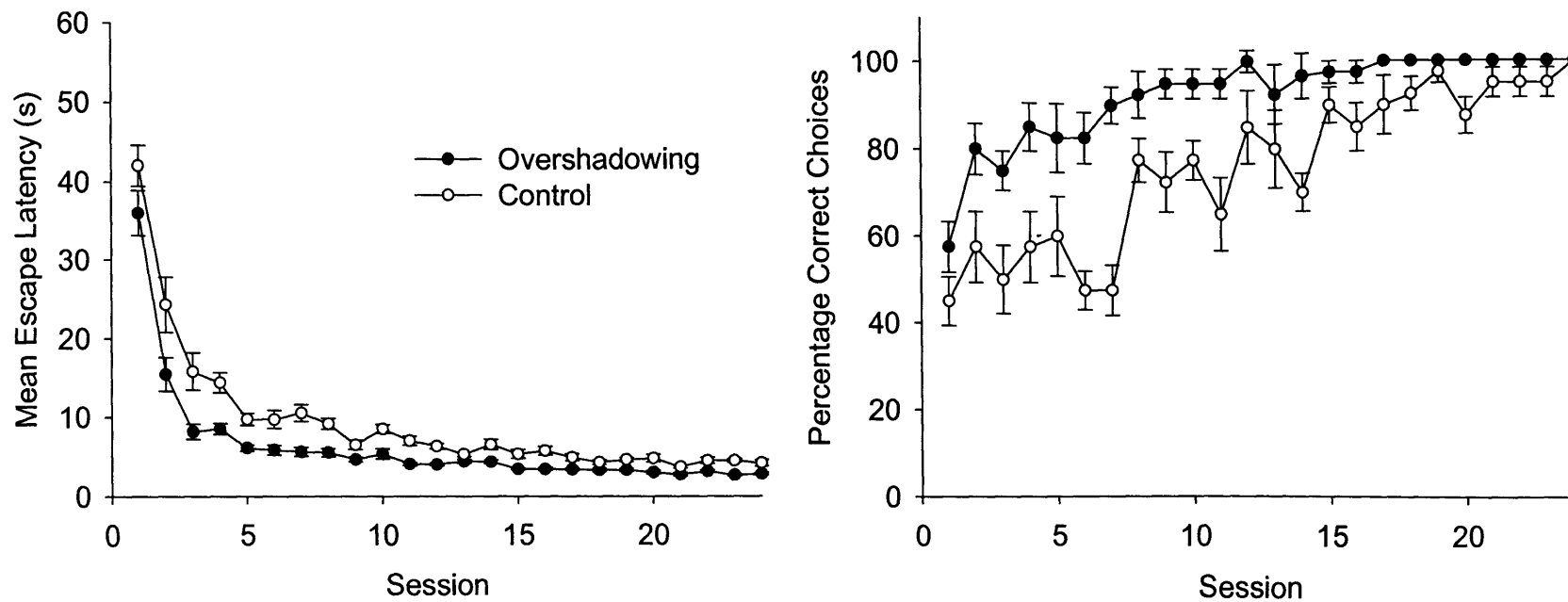


Figure 2.10. Mean (+SEM) escape latencies (left-hand panel) and mean (+SEM) percentage of correct choices (right-hand panel) for the overshadowing and control groups of Experiment 4.

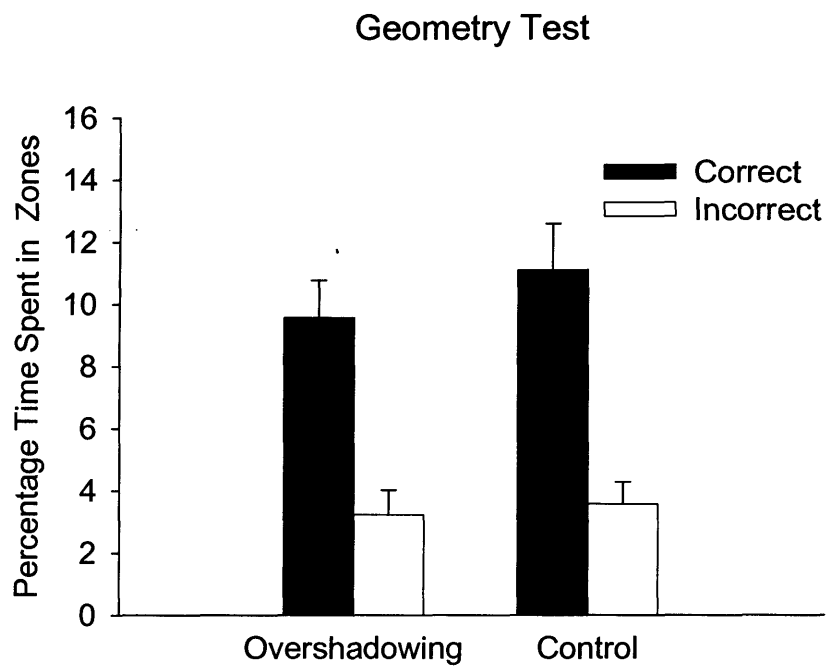


Figure 2.11. Mean (+SEM) percentage of time spent in the correct and incorrect zones during geometry test trial for the overshadowing and control groups of Experiment 4.

As with the last test trial in Experiment 3, the present results show a small hint of overshadowing. In order to determine if this effect is meaningful, an analysis was conducted in which the test results from this experiment and the results from the last test trial from Experiment 3 were combined, creating two groups of equal size ($n = 19$). An overall 2 X 2 (Group X Zone) ANOVA revealed a significant effect of zone, $F(1, 36) = 69.96$, but the main effect of group and the Group X Zone interaction was not significant, $F_s < 1.54$. It is possible with extended training, we would find an overshadowing effect, however even when we combined two sets of data to increase the sample size, and thus increase power of the statistical analysis, no overshadowing effect emerged. Also, the latency and choice data had reached a stable asymptote for each group and thus extended training would not be likely to result in any additional learning.

In conjunction with Experiment 3, the results of this experiment clearly show that a landmark does not restrict learning about geometric cues even when the salience of the geometric cues is substantially reduced. As with Experiment 1, the results fail to support the predictions from Miller and Shettleworth's (2007) model. It thus appears that a Rescorla-Wagner (1972) type of learning process may not provide a complete account of how animals learn about the location of a hidden goal in environments with distinctive shapes.

2.6. Summary and Conclusions

The main purpose of these experiments was to provide a test of Miller and Shettleworth's (2007) associative model of geometry learning. Their model predicts geometric cues should be overshadowed by a landmark when performance is compared against the two-landmark control group used in the present experiments. However, no support for this prediction was found. Even when the salience of the geometric cues was reduced, the landmark still failed to overshadow learning about the significance of geometric

cues (Experiment 3 and 4). The results suggest at best that Miller and Shettleworth's model provides an incomplete account for the acquisition of associative strength by cues in the spatial domain.

There is one concern with the manipulation of salience in the reported experiments. One could argue that the salience of geometric cues was not decreased enough in order to empirically observe overshadowing. This is unlikely considering that the results of Experiment 2 clearly showed a difference in acquisition of learning the significance of geometric cues when a group with high salient geometric cues was compared with a group with low salient cues. This difference was also apparent in the time spent in a circular search zone positioned in the correct location during test trials. These findings demonstrate forcefully that moving the platform away from the corner reduced the salience of the relevant geometric cues for locating the platform. Therefore, these results provide a problem for Miller and Shettleworth's model. I shall consider implications of these findings with respect to their model in the final chapter.

Spatial navigation is clearly a complex behaviour. Miller and Shettleworth (2007) argue the importance of cue competition in the acquisition of the behaviour. However, the present chapter has shown that Miller and Shettleworth provide an incomplete account of navigating in environments with distinctive shapes. Before drawing any further conclusions, we continue our analysis of Miller and Shettleworth's model in Chapter 3 with a theoretically more sensitive test of cue competition.

Chapter 3: A landmark blocks searching for a hidden platform in an environment with a distinctive shape after extended pre-training

3.1. Introduction

As we saw in Chapter 2, a landmark failed to overshadow learning about geometric cues, even when the salience of geometric cues was reduced. Miller and Shettleworth (2007) clearly predicted overshadowing in such an instance where the salience of the geometric cues was markedly reduced compared to the salience of the landmark. From these results, it is clear that manipulating the relative salience of the cues involved does not result in cue competition between landmarks and geometric cues, inconsistent with the model of Miller and Shettleworth. One could argue that an overshadowing design is not a sensitive test to which to measure cue competition. Even if geometric cues and landmarks do compete for control they acquire over spatial behaviour, it may be difficult to detect with an overshadowing paradigm. Thus, in the current chapter, we turn to a theoretically more sensitive test of cue competition, blocking, to assess the claim that spatial learning in environments with a distinctive shape are governed by the principles of associative learning and in doing so further evaluate the model proposed by Miller and Shettleworth.

Blocking has been observed in many species including fish (Tennant & Bitterman, 1975), birds (Mackintosh & Honig, 1970) and mammals (Kamin, 1969a; 1969b). Blocking has also been found with such diverse procedures as taste aversion conditioning (Willner, 1978) and the acquisition of casual judgments (Dickinson, Shanks, & Evenden, 1984). However, when an animal is trained to find a goal in the presence of a landmark in the first stage of a blocking experiment, and then trained to find a goal in the presence of the same landmark and geometric cues created by the shape of the environment in a subsequent stage, the landmark rarely ever successfully blocks learning about geometric cues (e.g., Hayward et al., 2003; Wall et al., 2004). Apart from the one instance of blocking of geometric cues

(Pearce et al. 2006), all other studies failed to show blocking. I shall return later to discuss the implications of the findings by Pearce et al., but for the time being we focus on one possible explanation for the failures to find blocking of geometric cues. Miller and Shettleworth (2007) have suggested that pre-training with a non-geometric cue should block learning about a geometric cue provided by the shape of the environment, if they should both subsequently signal where a goal can be found. To explain the failures to confirm this prediction, it was proposed by Miller and Shettleworth that the non-geometric cue lacked sufficient associative strength when it was paired with the geometric cue.

According to current theories of learning (e.g., Rescorla & Wagner, 1972) blocking will be more effective, and hence more likely to be detected, when the associative strength of the blocking cue is high at the outset of Stage 2. There are at least two reasons why the associative strength of the landmark might have been low at the start of Stage 2 in the experiments where blocking of geometric cues was not observed. First, the change in context from Stage 1 to Stage 2 might have resulted in a generalisation decrement in the associative properties of the landmark. In all reported spatial blocking experiments with geometric cues there was a change of contexts between Stages 1 and 2. For instance, Pearce et al. (2001) trained rats to locate a platform with a beacon attached to it during Stage 1 in a circular pool and then trained rats to find the platform in one corner of a triangular pool with the beacon still attached to the platform. The change in context between Stages 1 and 2 may have disrupted the association between the beacon and the location of the platform formed during Stage 1 and thus decreased the likelihood of detecting blocking. Second, it is possible that there was insufficient training with the landmark during Stage 1. The number of Stage-1 training trials in the experiments that failed to reveal blocking varied between 20 (Pearce et al., 2001) and 56 (Wall et al., 2004). Even though there was evidence in these experiments that this training was sufficient to encourage rats to approach the blocking cue, it is possible

that the associative properties of the cue were just sufficient to produce this effect, and still some considerable distance from an asymptotic value that would be achieved if substantially more training had been given.

The present experiments explored both of these possibilities for the failure of a landmark to block geometric cues. By conducting Stage 1 and Stage 2 in the same context, Experiment 5 attempted to minimise the possibility that blocking of geometric cues would fail because of generalisation decrement. Experiments 6 and 7 examined the effects of using extended Stage-1 training with the aim of increasing the likelihood that the associative strength of the landmark will be high at the outset of Stage 2 and thus enable it to serve as an effective cue for blocking.

3.2. Experiment 5

A blocking group received Stage 1 in the triangular-shaped pool used in Experiments 1-4 with a submerged escape platform located randomly in one of the two equal-angled corners. A spherical landmark was always located above the platform no matter its location. During this stage, only the landmark could be used to locate the platform. For the second stage, this group received the platform located in just one of the equal-angled corners of the triangle beneath the same landmark. Both Stages 1 and 2 occurred in the same context to minimise generalisation decrement as a result of the transition from Stage 1 to Stage 2, and presumably maintain the high associative strength of the spherical landmark. Two control groups were trained identically in Stage 1 to the blocking group, except that a rod-shaped landmark was attached to the platform. In Stage 2, the control groups were trained with the platform in one of the corners at the base of the triangle, where only geometry was the reliable indicator of the location of the platform. To equate the three groups as closely as possible for the change they experienced at the transition from Stage 2 to the final test trial,

each control group was exposed to one or two spherical landmarks that were unreliable cues for finding the platform. For one control group, a single landmark was located randomly across trials in each of the two equal-angled corners of the pool. A second control group was trained in Stage 2 with two identical landmarks, one over the correct corner that contained the platform and one in the opposite, incorrect, corner. In order for the control groups to find the platform accurately, the geometric cues of the correct corner must be relied upon. Following training, all groups received a 60-s test trial in a triangular pool with the platform and landmarks removed.

It must be noted that the typical control for a blocking experiment, where the control group receives the exact same training as the experimental group during Stage 2, was omitted in this experiment. With the traditional control, the possibility of observing blocking in the blocking group may be diminished because overshadowing by the landmark in the control group might reduce, perhaps considerably, the associative strength of the geometric cue. Both of the chosen control groups do not pose this problem. In order for the two control groups to master their tasks, they must learn about the location of the platform with respect to the geometry of the environment. The possibility of observing blocking will then be enhanced as the associative strength of the target cue will theoretically be at a higher value than if the conventional control condition had been employed. These are particularly strong control groups if a null result is observed.

3.2.1. Method

Subjects and Apparatus. The 27 rats were from the same stock, of approximately the same weight, and housed in the same manner as in Experiment 1. All rats were previously trained in an appetitive conditioning experiment and had no previous training in a swimming pool. The apparatus, which consisted of a triangular pool with a curved base was identical to

Experiment 1 except in this experiment two different types of landmarks were used. One landmark, attached to the platform, consisted of a plastic rod painted with alternating black and white, 1 cm wide hoops. A white disk, 3 cm in diameter and 0.5 cm thick, was attached to the top of the landmark. This landmark was attached to the platform, 2.5 cm from its edge. The other landmark was the same black sphere used in Experiment 1.

Procedure. There were two stages of training in the experiment. Stage 1 and Stage 2 consisted of 12 and 14 sessions of training respectively.

Rats were randomly assigned to three groups in equal numbers ($n = 9$): blocking, control-1 and control-2 (where 1 and 2 refer to the number of landmarks present during Stage-2 training). During Stage 1, all rats in the blocking group received the spherical landmark directly over the platform in the corner where the long wall was to the left of the curved wall for half of the trials and for the remaining trials the platform and spherical landmark were in the corner where the long wall was to the right of the curved wall. The location of the platform and landmark varied randomly with the requirement that each corner was used twice in a given session. Both control groups received the same training, except that the spherical landmark was replaced with a rod-shaped landmark attached to the platform. After 12 sessions of training, all rats proceeded to Stage 2.

During the 14 sessions of Stage 2, for the blocking group five of the rats always had the spherical landmark over the platform in the corner where the long wall was to the left of the curved wall, while the remaining four rats had the spherical landmark and the platform in the corner where the long wall was to the right of the curved wall. For the control-1 and control-2 groups, the platform was located in the same place as the blocking group. The only difference between the control groups was that the control-1 group had one spherical landmark randomly positioned in one of the two corners at the base of the triangle with the stipulation that each corner was used twice during a given session and that the spherical

landmark was above the platform for half the trials in each session. The control-2 group had two identical spherical landmarks each located in the two corners at the base of the triangle. The landmarks were always positioned so that the centre of the sphere was situated 25 cm from the correct corner on a line that bisected the corner (i.e., directly over the area where the platform would be placed). The first three trials of session 14 in Stage 2 were conducted in the same manner as previous trials. The fourth trial of session 14 was a geometry test. During this test trial, the platform and all landmarks were removed from the pool. The rats were placed in the centre of the arena and allowed to swim for 60 s.

As in Chapter 2, latencies to find the platform on each trial were recorded and revealed results entirely in keeping with choices and as such will not be reported for the present and remaining chapters of this thesis where choices can be recorded. In general, latencies to find the platform provide no additional information beyond what can be inferred from the analysis of choices across training trials. In instances where choices cannot be recorded due to an experimental design reason then latencies will then be reported as a measure of acquisition across training. Any other procedural details omitted were identical to Experiment 1.

3.2.2. Results and Discussion

The left-hand panel of Figure 3.1 shows the mean percentage of correct choices for the three groups during the 12 sessions of Stage 1. At first, performance was rather poor, but all three groups rapidly acquired the response of heading to the correct corner after being released into the pool. To compare the performance of the three groups, individual mean percentages of trials on which a correct choice was made for the last three sessions combined were calculated. A Kruskal-Wallis test based on these individual means revealed no significant difference among the groups, $H(3) = 2.21$.

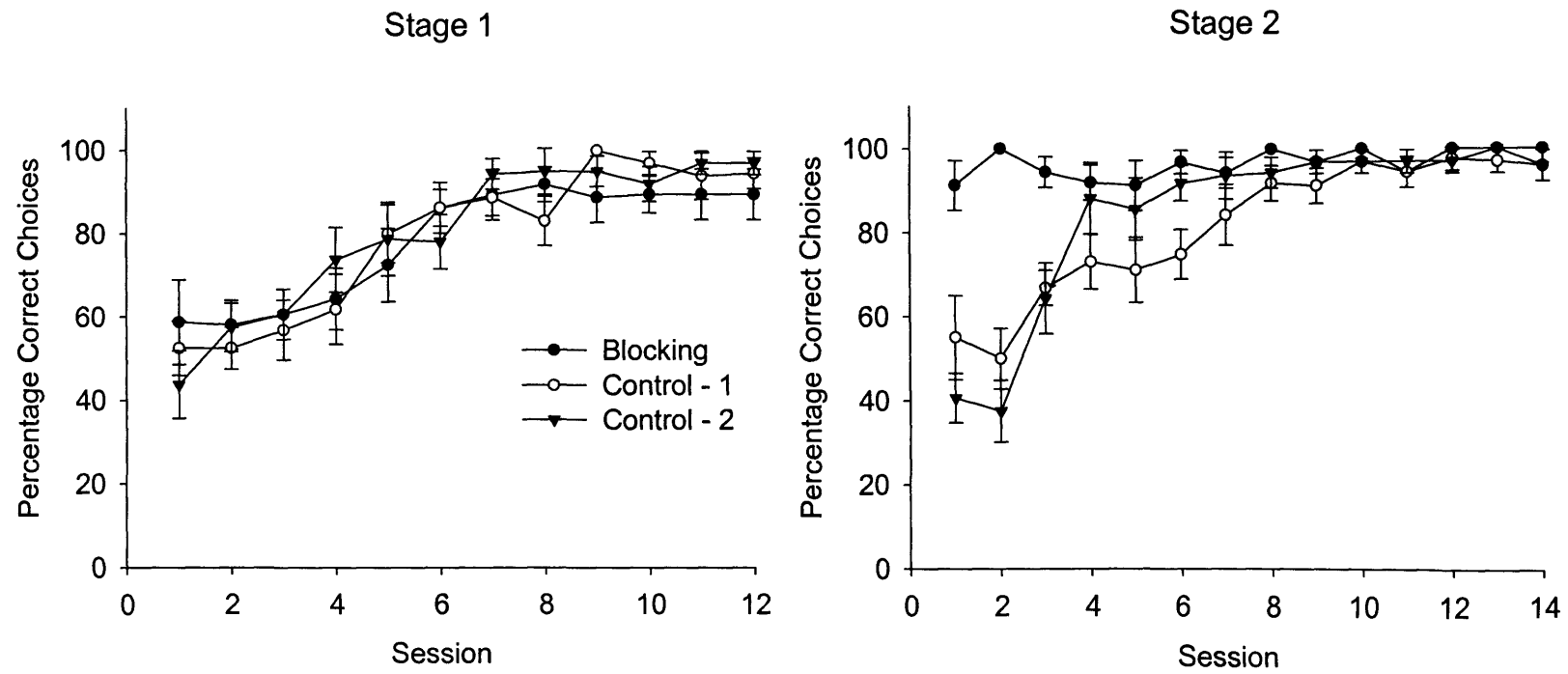


Figure 3.1. Mean (+SEM) percentage of correct choices across Stage 1 (left-hand panel) and Stage 2 (right-hand panel) for the blocking, control-1 and control-2 groups of Experiment 5.

The right-hand panel of Figure 3.1 shows the mean percentage of correct choices for the three groups during the 14 sessions of Stage 2. As can be seen, the blocking group showed excellent transfer of behaviour from Stage 1 compared to the control groups. This was confirmed by a Kruskal-Wallis analysis on the individual mean percentages for first three sessions combined, $H(3) = 18.3$. The blocking group was significantly different than both the control groups, $Us(9, 9) < 0.6$, but the control-1 and control-2 groups did not differ, $U(9, 9) = 26.0$. However, by the end of training, all groups performed similarly as confirmed by a Kruskal-Wallis analysis on individual mean percentages for the last three sessions combined, $H(3) = 3.23$.

The mean time spent in the correct and incorrect zones for the geometry test are shown in Figure 3.2. All three groups spent substantially more time in the correct than the incorrect zone, but the extent of the preference was somewhat less pronounced for the blocking than the control groups. A 3 X 2 (Group X Zone) ANOVA revealed a significant main effect of zone, $F(1, 24) = 57.72$. The remaining analysis revealed non-significant effects for group, $F(2, 24) = 1.38$, and a non-significant Group X Zone interaction, $F(2, 24) = 1.39$.

The purpose of this experiment was to test whether the failure of a landmark to block learning about geometric cues was a result of a generalisation decrement, due to a change in context between Stage 1 and 2, which reduced the associative strength of the blocking cue. Stages 1 and 2 of the present experiment were conducted in the same context and there was still no evidence of blocking. This result indicates that generalisation decrement, as a result of changing contexts between Stages 1 and 2, was not responsible for the failure to observe blocking in the studies by Hayward et al. (2003; 2004), Pearce et al. (2001) and Wall et al. (2004). An alternative explanation for the failure in these studies, and the present one, to reveal blocking is that insufficient training was given in Stage 1 for the associative strength

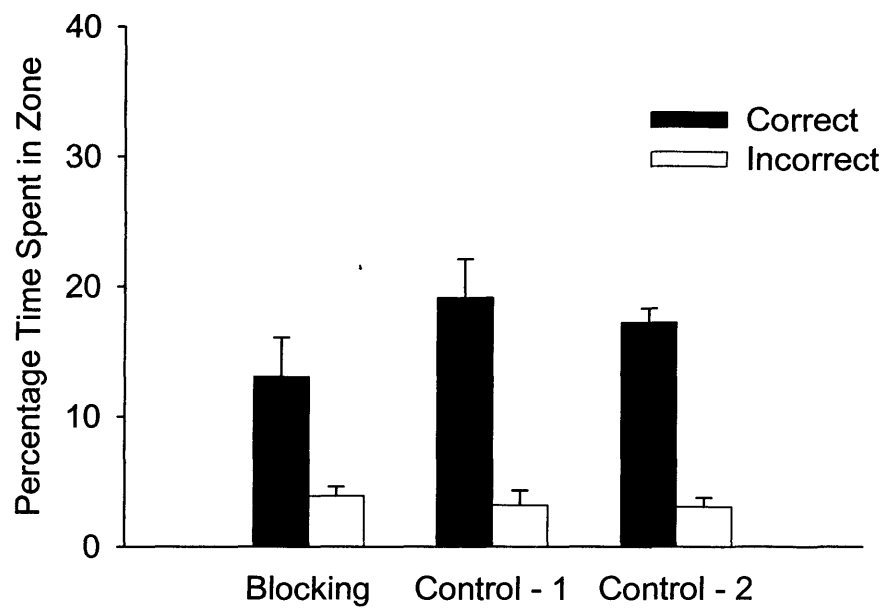


Figure 3.2. Mean (+SEM) percentage of time spent in the correct and incorrect zones during the geometry test for the blocking, control-1 and control-2 groups of Experiment 5.

of the blocking cue to reach asymptote. An obvious way to test this explanation would be to extend the length of training with the blocking cue in Stage 1, which served as the rationale for Experiments 6 and 7.

3.3. Experiment 6

Experiment 6, was similar to Experiment 5, except there was only two groups and that the number of Stage-1 sessions was increased to 24 in the hope that the additional training will enhance the associative strength of the landmark to such an extent that it will block the geometric cues.

3.3.1. Method

Subjects and Apparatus. The 16 rats were from the same stock, of approximately the same weight, and housed in the same manner as in Experiment 5. All rats were previously used in an appetitive conditioning experiment and had no previous training in the swimming pool. At the start of the experiment they were assigned randomly in equal numbers to two groups. The apparatus was the same as in Experiment 5.

Procedure. The control group was trained in an identical manner to the control-2 group in Experiment 5 and the blocking group was trained in the same manner as its namesake in that experiment. The only difference between the experiments was that there were 24, rather than 12 sessions in Stage 1. Stage 2 consisted of 14 sessions of training. The fourth trial of Session 14 of Stage 2 was a geometry test, conducted in the same manner as in Experiment 5.

3.3.2. Results and Discussion

The left-hand panel of Figure 3.3 shows the mean percentage of correct choices for the two groups during the 24 sessions of Stage 1. As was seen in Experiment 5, both groups started poorly, but eventually acquired the response of heading directly to the correct corner on virtually every trial. To compare the performance of the two groups, individual mean percentages of trials on which a correct choice was made for the last three sessions combined were calculated. A Mann-Whitney U test based on these individual means revealed no significant difference between the groups, $U(8, 8) = 21.50$.

The right-hand panel of Figure 3.3 shows the mean percentage of correct choices for the two groups during the 14 sessions of Stage 2. Similar to Experiment 1, the performance of the control group was impaired at the beginning of Stage 2 relative to the blocking group. To compare the performance of the two groups, individual mean percentages of trials on which a correct choice was made for the first three sessions combined were calculated and revealed a significant difference, Mann-Whitney $U(8, 8) = 0$. However, as was shown in the previous experiment, by the end of training the two groups were performing equivalently. A Mann-Whitney U analysis on the individual mean percentages for last three sessions combined confirmed there was no difference between the groups, $U(8, 8) = 23.00$.

Figure 3.4 shows the results from the geometry test. The blocking group spent a smaller proportion of time in the correct zone compared to the control group. A 2 X 2 (Group X Zone) ANOVA revealed a significant effect of group, $F(1, 14) = 8.57$, zone, $F(1, 14) = 60.27$, and a significant Group X Zone interaction, $F(1, 14) = 8.37$. A simple effects analysis of the interaction revealed that the blocking group spent significantly less time in the correct zone than the control group, $F(1, 28) = 16.53$. Both groups also spent significantly more time searching for the platform in the correct zone than the incorrect zone, $F_s(1, 14) > 11.86$.

Extended Stage-1 training with the landmark resulted in the blocking group spending

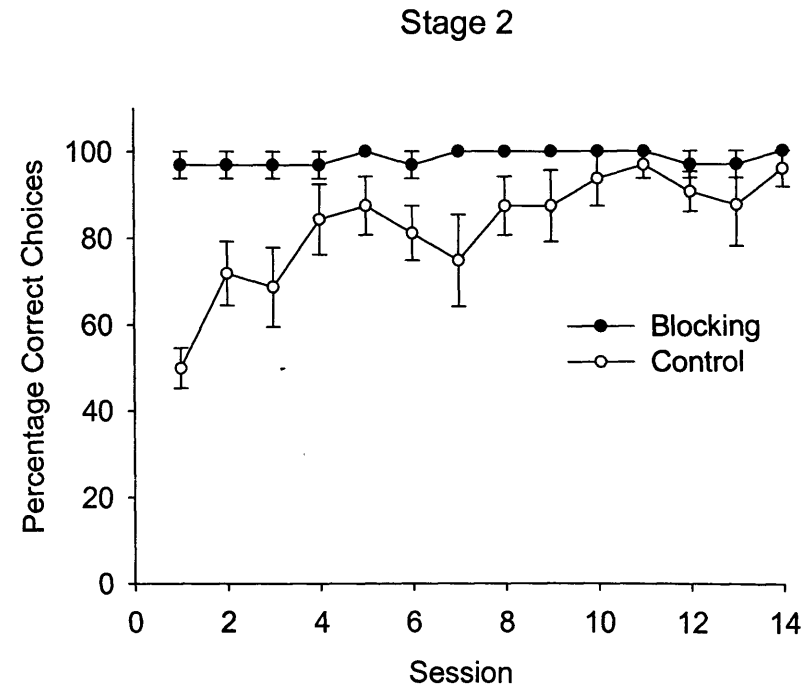
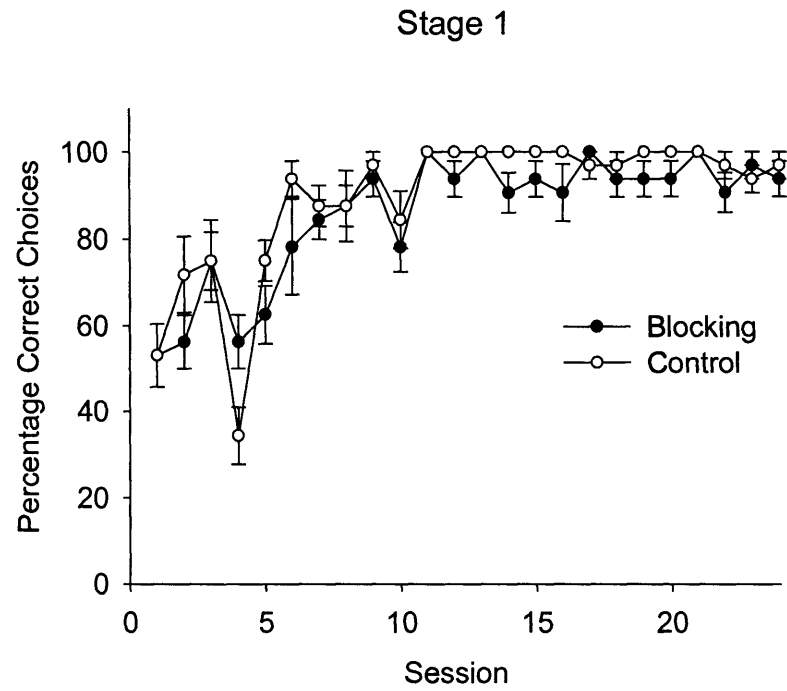


Figure 3.3. Mean (+SEM) percentage of correct choices across Stage-1 (left-hand panel) and Stage-2 (right-hand panel) training for the blocking and control groups of Experiment 6.

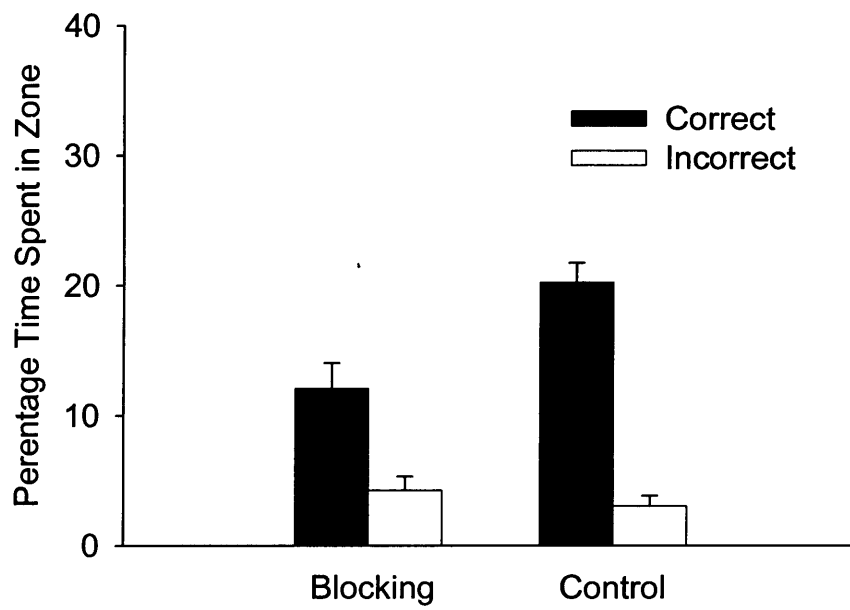


Figure 3.4. Mean (+SEM) percentage of time spent in the correct and incorrect zones for the blocking and control groups during a geometry test trial of Experiment 6.

significantly less time than the control group in the vicinity of the correct corner during the test trial. The results demonstrate that when there are 24 sessions of training with the landmark during Stage 1 of a blocking experiment, it can block learning about geometric cues during the second stage of the experiment. This finding thus constitutes the first demonstration with animals that the presence of a landmark, given suitable training, can block learning about geometric cues (for a similar demonstration of blocking with humans see Wilson & Alexander, 2008). It now becomes important to consider how such blocking took place. According to the model of Miller and Shettleworth (2007), the extensive pre-training with the landmark endowed it with sufficient associative strength to enable it to restrict learning about the geometric cues, because both sets of cues were in competition for a limited amount of associative strength (Rescorla & Wagner, 1972). It is possible that extended training did in fact increase the associative strength of the landmark. However, it is possible to explain the present results in a rather different way. Note that the training in Stages 1 and 2 took place in the same triangular environment. According to the theory of Mackintosh (1975), the protracted Stage-1 training will result in attention to the geometric cues being low because they were irrelevant for finding the platform (Mackintosh, 1973). On the other hand, attention to the landmark used in Stage 1 will be high because of it being a reliable cue for finding the platform. Upon the introduction of Stage 2, the experimental group, according to this theory, will continue to pay attention to the landmark and ignore the geometric cues and, despite now being relevant, the geometric cues should gain little associative strength. In contrast, the introduction of a new landmark at the outset of Stage 2 for the control group will result in neither the landmark nor the geometric cues being good predictors of where the platform can be found. As a consequence, the theory predicts that attention to the geometric cues will increase and permit them to gain more associative strength than in the experimental group.

Support for the above account can be found in reports by Prados, Redhead and Pearce (1999), and Redhead, Prados and Pearce (2001). Redhead et al. (2001), for example, trained two groups of rats to swim to a submerged platform beneath a landmark in a circular pool while they could view the stimuli provided by the room housing the pool. For one group, the platform remained in the same place for the four trials of each session, whereas for another group the platform was moved from trial to trial. The room cues were thus relevant for locating the platform within a session for the first but not the second group. During a subsequent test with the platform in a fixed location for both groups, but without the landmark, the first group showed a more rapid decline in escape latencies across trials than the second group. Redhead et al. attributed this outcome to the different treatments resulting in the first group paying more attention to the room cues than the second group at the outset of the test trials.

3.4. Experiment 7

The results from Experiment 6 demonstrate blocking, but it is not clear whether this effect was a consequence of stimuli competing for associative strength or to changes in attention to the geometric cues. As a step towards evaluating these explanations, the present experiment was based on the design of Experiment 6, except that the training in Stage 1 was conducted in a circular rather than triangular pool. Provided that the training in Stage 1 endows the landmark with sufficient associative strength, the model of Miller and Shettleworth (2007) predicts that blocking will be observed after training in either environment. On the other hand, in the present experiment, the novelty of the geometric cues at the outset of Stage 2 can be expected to encourage the blocking group to pay them considerable attention and according to the attentional explanation that has just been developed, the likelihood of now observing blocking will be reduced.

A comparison of the results from Experiments 5 and 6 implies that the landmark blocked learning about the geometric cues when there were 24, but not when there were 12 sessions of training in Stage 1. In order to confirm this conclusion, the present experiment included groups that received 12 and 24 sessions of training in Stage 1. The experiment therefore contained four groups. The four groups were initially trained in a circular swimming pool during Stage 1. The two blocking groups received a spherical landmark directly above the platform, randomly positioned across trials, in one of the four quadrants of the pool. One group received 12 sessions and the other received 24 sessions. The two control groups received the same training, but rather than the spherical landmark, they received a rod-shaped landmark attached to the platform. Stage 2 was conducted in the same way as for the blocking and control groups of Experiment 6.

In addition to the geometry test, landmark tests were conducted to give an indication of the associative strength acquired by the spherical landmark for each of the four groups. Groups of particular interest are the blocking groups because the associative strength of the landmark should differ according to the amount of training given in Stage 1, if blocking is found in the group that received more Stage-1 training.

3.4.1. Method

Subjects and Apparatus. The 32 rats were from the same stock, of approximately the same weight, and housed in the same manner as in Experiment 5. All rats were previously used in an appetitive conditioning experiment and had no previous training in the swimming pool. At the start of the experiment they were assigned randomly in equal numbers to four groups. The apparatus was the same as in Experiment 5.

Procedure. All procedures were identical to that of Experiment 6 with the exception that Stage 1 was conducted in a circular pool rather than a triangular pool and that half the

rats received 12 sessions of Stage-1 training (groups control-12 and blocking-12) and the other half received 24 sessions (groups control-24 and blocking-24). Groups that received 24 sessions of Stage-1 training were started 12 days prior to those that received 12 sessions to ensure that Stage 2 commenced on the same day for all rats. During Stage 1, the control groups received the rod attached to the platform, which was placed randomly in a different quadrant of the circular pool, with the only stipulation that each quadrant of the pool was used once within a session. The platform was positioned 25 cm or 50 cm from the side of the pool, each for two trials per session. The platform was randomly located across trials in each quadrant of the pool (NE, NW, SW, SE) with the stipulation that each quadrant was used once per session. Similarly, rats were released into the pool from the cardinal compass points (N, E, S, W). Each release point was used once within a session. The blocking groups received identical treatment except that the landmark was a sphere suspended directly over the platform. Stage 2 was conducted in the same manner as in Experiment 6 and contained 16 sessions. The last trial of Session 14 of Stage 2 was a geometry test, conducted in the same manner as in Experiment 5. The first three trials of Session 16 were conducted in the same manner as previous trials. The fourth trial was a landmark test. For this test trial the platform and the walls forming the triangular-shaped pool were removed. The spherical landmark was hung 50 cm from the edge of the circular pool. A circular search zone (30 cm in diameter) directly under the landmark was used to analyze the results from this test. Session 16 was then followed by three similar tests with the landmark at the rate of one per day, but with only the two blocking groups because for the two control groups the landmark was an unreliable predictor for the location of the platform and thus the amount of control acquired by the landmark in the control groups was expected to be very small.

3.4.2. Results and Discussion

The left-hand panel of Figure 3.5 shows the mean escape latencies for the four groups during the 24 sessions of Stage 1. In contrast to the previous experiments we did not record choices during Stage 1 because it took place in a circular pool. All groups learned rapidly to swim to the platform by the end of the stage. A 2 X 2 (Group X Session) ANOVA conducted on the individual mean escape latencies combined across the last three sessions revealed significant effects of group, $F(1, 28) = 48.59$, and session, $F(1, 28) = 7.15$, as well as a significant Group X Session interaction, $F(1, 28) = 6.07$. An analysis of the interaction revealed that the blocking-12 group took significantly longer to find the platform than the blocking-24 group, $F(1, 28) = 13.20$, but the control-12 and control-24 groups did not differ, $F < 1$. Given that the blocking-24 group found the platform faster than the blocking-12 group, it could be inferred that extended training was effective in the blocking-24 group resulting in the associative strength of the sphere being greater in this group than in the blocking-12 group. The right-hand panel of Figure 3.5 shows the mean percentage of correct choices for the four groups during the 16 sessions of Stage 2. At first, the control groups made a correct choice on approximately half of the trials, whereas the blocking groups made a correct choice on the majority of trials from the outset of Stage 2. This initial difference among the groups was confirmed by a Kruskal-Wallis analysis based on the individual means of correct choices combined across the first three sessions, $H(4) = 23.99$. Mann-Whitney U tests revealed that the blocking-24 and blocking-12 groups did not differ, $U(8, 8) = 23.0$, and the control-24 and control-12 groups did not differ, $U(8, 8) = 15.5$. All other comparisons revealed a difference between the groups, $U(8, 8) < 1.1$. However, by the end of Stage-2 training, a Kruskal-Wallis test based on individual means of correct choices combined across the last three sessions before the first test trial revealed no significant difference among the groups, $H(4) = 6.55$.

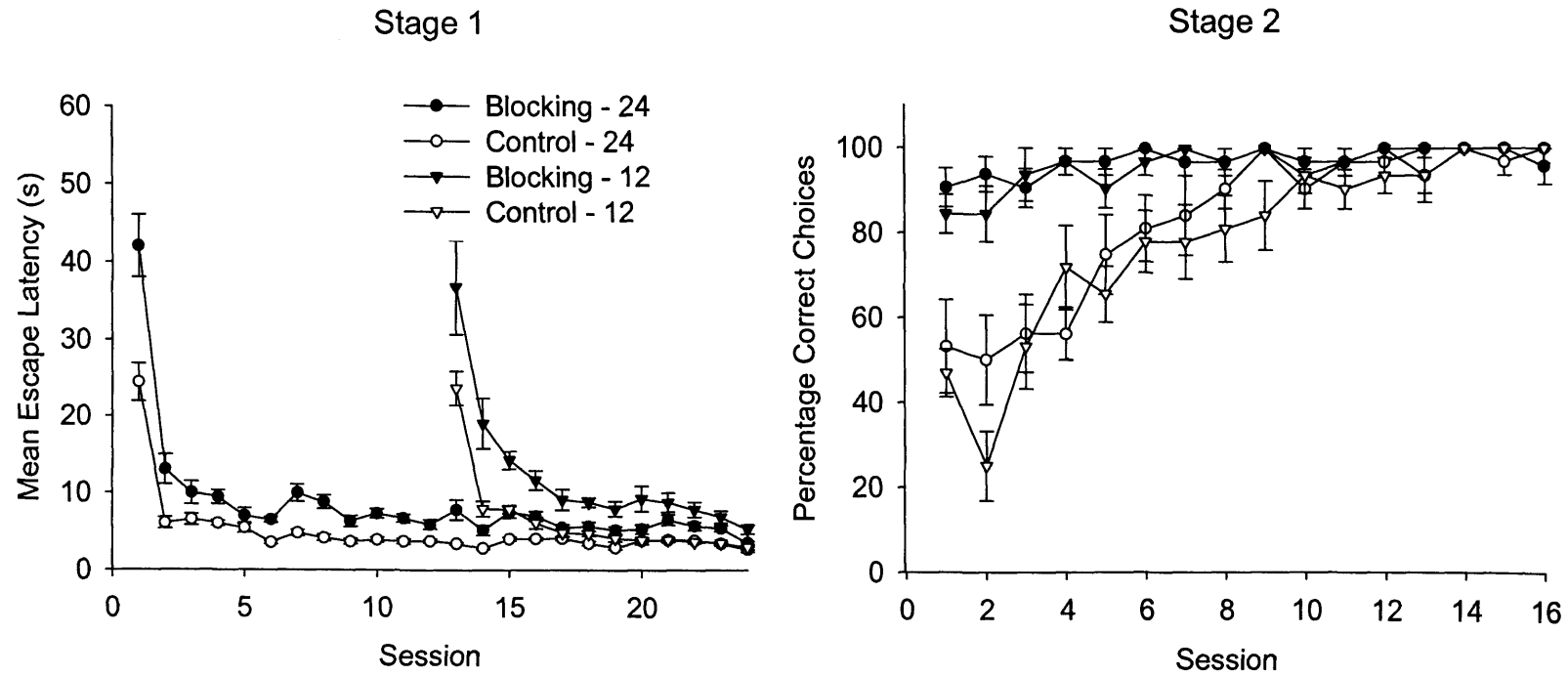


Figure 3.5. The left-hand panel shows the mean (+SEM) escape latencies to find the hidden platform across Stage-1 training for the blocking and control groups of Experiment 7. The right-hand panel shows the mean (+SEM) percentage of correct choices made across Stage-2 training for the blocking and control groups of Experiment 7.

The left-hand panel of Figure 3.6 shows the time spent searching in the correct and incorrect zones for all four groups during the geometry test. It is obvious that the blocking-24 group spent less time in the correct search zone than its respective control, while the blocking-12 and control-12 groups spent an equal amount of time in the correct zone. A 2 X 2 X 2 (Group X Session X Zone) ANOVA was conducted (where group refers to blocking or control; session refers to 12 or 24 sessions during Stage 1; zone refers to correct or incorrect zones). The analysis revealed a significant effect of group, $F(1, 28) = 4.57$, and zone, $F(1, 28) = 121.67$. There were also significant two-way interactions of Group X Session, $F(1, 28) = 7.51$, and Group X Zone, $F(1, 28) = 12.41$. However, more importantly, there was a significant Group X Session X Zone three-way interaction, $F(1, 28) = 5.25$. The remaining findings from the ANOVA were non-significant, $F_s < 1$.

Simple effects analysis of the three-way interaction revealed that groups control-24 and blocking-24 differed in the percentage of time spent in the correct zone, $F(1, 56) = 28.80$. This difference was not present in groups that received only 12 session of training in Stage 1, $F < 1$. Also, the blocking-24 group spent significant less time in the correct zone than the blocking-12 group, $F(1, 56) = 4.91$. Unexpectedly, the control-12 group spent significantly less time in the correct zone compared to the control-24 group, $F(1, 56) = 7.57$.

The right-hand panel of Figure 3.6 shows time spent in the correct zone during the landmark test. The blocking groups spent a larger proportion of time searching directly under the landmark compared to the control groups. A 2 X 2 ANOVA (Group X Session) revealed a significant group effect, $F(1, 28) = 33.87$. The session effect and Group X Session interaction were non-significant, $F_s < 1$.

Figure 3.7 shows the time spent searching in the correct zone for the blocking-24 and blocking-12 groups across the 4 consecutive landmark tests. As can be seen, both groups spent less time searching under the landmark across trials. A 2 X 2 (Group X Trial) ANOVA

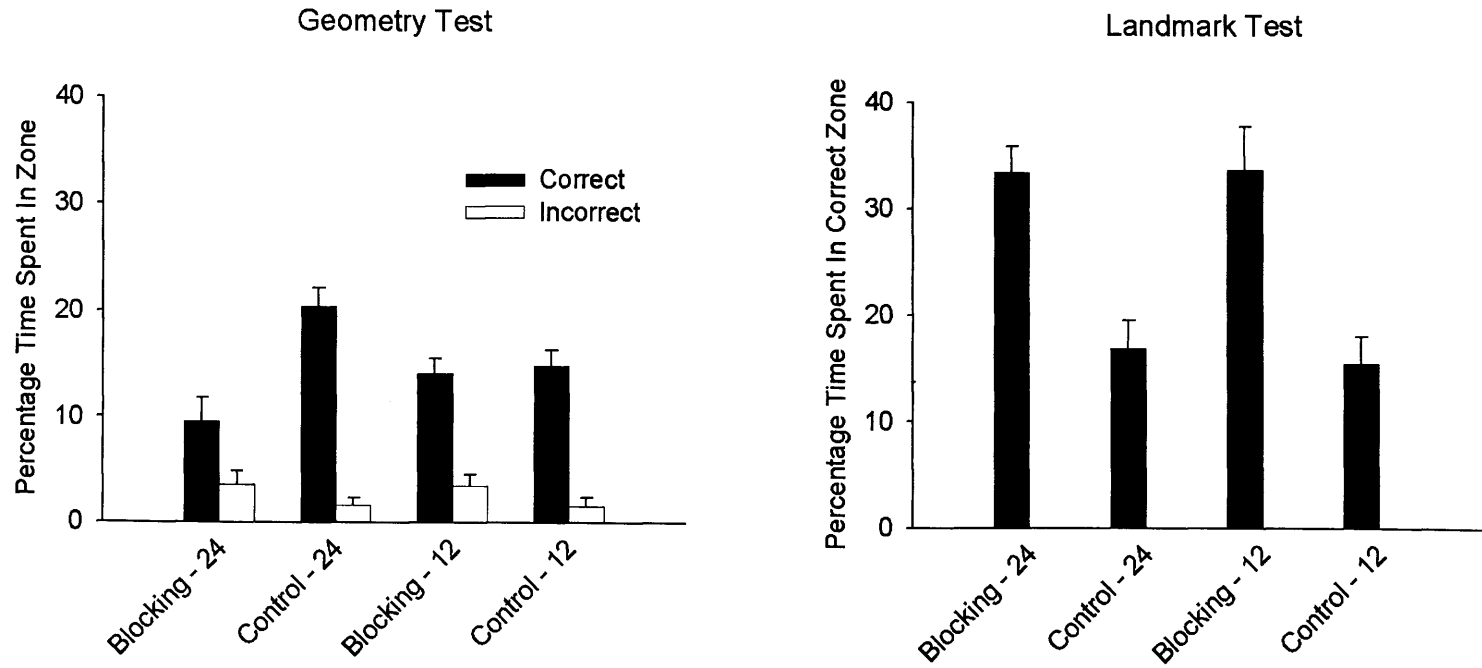


Figure 3.6. Left-hand panel: Mean (+SEM) percentage of time spent in the correct and incorrect zones during a geometry test trial for the four groups of Experiment 7. Right-hand panel: Mean (+SEM) percentage of time spent in the correct zone during the landmark test for the four groups of Experiment 7.

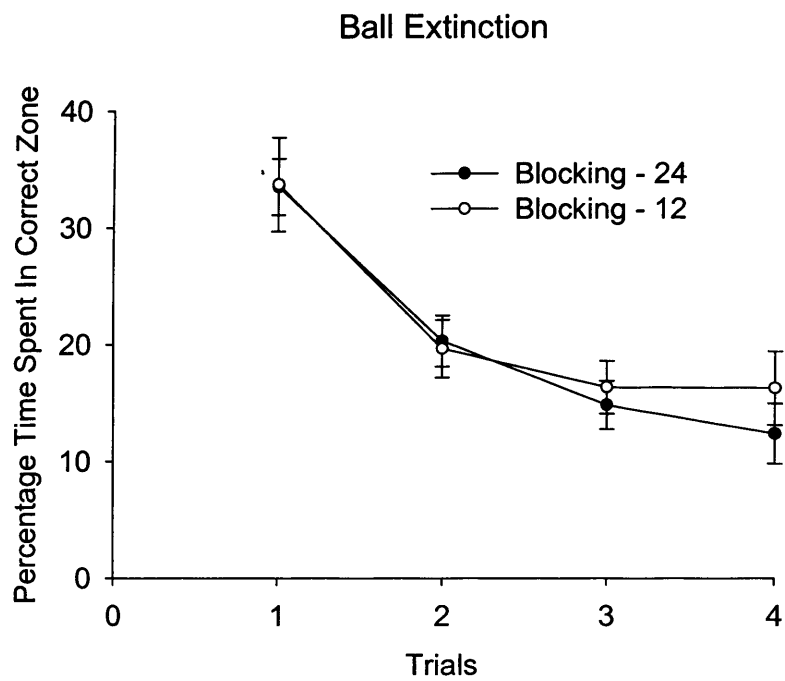
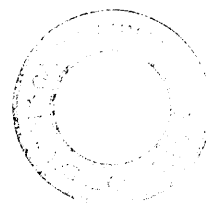


Figure 3.7. The mean (+SEM) percentage of time spent in the correct zone for the four extinction trials of the landmark for the blocking-24 and blocking-12 groups of Experiment 7.



confirmed these results. There was a significant effect of trial, $F(3, 14) = 29.81$. The group effect and the Group X Trial interaction were non-significant, $F_s < 1$.

The results obtained successfully replicate those found in Experiments 5 and 6. Rats that received 24 sessions of training with the spherical landmark during Stage 1 spent significantly more time in the correct corner during the test in the triangle than the control groups. This difference was not evident between the two groups trained for 12 sessions in Stage 1. The results suggest that the blocking effect observed in Experiment 6 does not depend upon a loss of associability by the geometric cues by virtue of them being present during Stage 1. According to this explanation, blocking in Experiment 6 occurred because the training in Stage 1 resulted in the blocking group failing to attend to the geometric cues in Stage 2. By introducing the triangular arena at the outset of Stage 2, it was anticipated its geometric features would be attended to by both groups, at least initially. These features would then be expected to acquire associative strength and make it difficult to reveal blocking in the blocking-24 group.

One unexpected finding from the experiment was that the control group which received 12 sessions of training in Stage 1 spent less time in the correct search zone during the test trial in the triangle than the control group which received 24 sessions of training in Stage 1. Both groups received the same amount of identical training during Stage 2 in the triangle, and there is thus no good reason to expect them to differ in the degree to which the geometric cues provided by the triangle controlled searching for the platform. It is difficult to think of a good explanation for this difference between the results of the two control groups, except that it was due to sampling error. Nonetheless, this unexpected finding does not affect the principal conclusions from the experiment. The significantly less time spent in the correct zone by the blocking-24 than the control-24 group during the first test demonstrates that

blocking was effective after 24 sessions of training in Stage 1. Furthermore, the difference between the results from the first test trial for the blocking-24 and the blocking-12 groups demonstrates that blocking was more effective after 24 than 12 sessions of Stage-1 training. A second unexpected finding from the experiment was the failure to find a difference between the two blocking groups during the tests with the landmark in the circular pool. The implications of this finding will be considered shortly.

3.5. Summary and Conclusions

The present set of experiments has provided the first demonstration of blocking of geometric cues by a discrete landmark in animals. In two experiments, it has been demonstrated that if rats are first trained to locate a submerged platform underneath a landmark for 24 sessions, then learning about the position of the platform with reference to the shape of the environment was blocked in a second stage, when both the shape of the environment and the landmark indicated where the platform could be found. Before considering the theoretical implications of these results, some discussion is needed as to whether the experiments actually revealed blocking.

The control groups in Stage 2 of Experiments 6 and 7 were trained with a spherical landmark in each of the corners at the base of the triangle with the platform beneath one of them. This treatment was different to the conventional control group for a blocking design, which would involve the same Stage-2 treatment as that given to the blocking group in order to control for overshadowing. An unconventional control condition was used because a failure to find a difference between the test results of the blocking and the control groups would reveal particularly forceful evidence that the blocking treatment did not restrict learning based on the geometric cues. As it turns out, there was a difference between the test results for the blocking and control groups in Experiments 6 and 7 and, given the design of

the control condition, it is impossible to claim with certainty that this difference was a consequence of blocking rather than overshadowing. That is, the pre-training with the landmark in Stage 1 may not have been responsible for the poor control over searching for the platform acquired by the geometric cues in Stage 2. Instead, this outcome may have occurred because the single landmark overshadowed the geometric cues during Stage 2 for the blocking group. Such overshadowing would not be anticipated for the control groups where the manner in which the landmarks were used meant that subjects had to rely on the shape of the pool for finding the platform. There are two reasons for believing that the difference between the blocking and control groups of Experiments 6 and 7 was not a consequence of overshadowing. On the one hand, there is no obvious reason why overshadowing in Stage 2 should be more effective after 24 than 12 sessions of Stage-1 training, yet this would have to be the case if the absence of blocking in Experiment 5 is to be explained. On the other hand, In Chapter 2, Experiment 1, two groups of rats were trained identically to the blocking and control groups of Experiments 6 and 7, except that the Stage-1 training was omitted, and there was no hint of overshadowing. It seems, therefore, that the difference between the effects of the control and blocking treatments in the present experiments depends upon extended training in Stage 1 with the spherical landmark, which implies that the outcome of Experiments 6 and 7 was a consequence of blocking rather than overshadowing.

We noted in the Introduction that blocking of geometric cues has been reported using the colour of the walls of a distinctively shaped arena as the additional cue for finding a hidden goal (Pearce et al., 2006). In contrast to the present experiments, this effect was reported with only 14 sessions of Stage-1 training. A possible explanation for the finding in the present studies that 24, but not 12 sessions of Stage-1 training was necessary in order to obtain blocking is that the salience of the, relatively small, spherical landmark was less than

of the, relatively large, black and white walls used in the study by Pearce et al. More initial training would then be required with the sphere than the black and white walls, in order to endow the sphere with sufficient associative strength for it to block the geometric cues.

The experiments were conducted in order to test the suggestion by Miller and Shettleworth (2007) that previous failures of a non-geometric cue to block geometric cues were a consequence of the former possessing inadequate associative strength at the start of Stage 2. Miller and Shettleworth further proposed that if the blocking cue should gain sufficient associative strength during Stage 1 then it will block spatial learning about the geometric cues for reasons that follow from the Rescorla-Wagner (1972) theory. The fact that blocking was effective after 24 but not 12 sessions of Stage-1 training is consistent with this claim but, as noted earlier, not all of our findings are compatible with this explanation for our results. For example, the test in the triangle at the end of Experiment 7 revealed that the blocking-24 group spent less time in the correct corner than the blocking-12 group. The implication of this finding is that the associative strength of the spherical landmark at the time of testing was greater in the blocking-24 than the blocking-12 group. However, a repeated series of test trials with the spherical landmark indicated that its associative properties were very similar in both groups. A possible explanation for this outcome is that the test for the associative properties of the sphere was insensitive. Although it is not possible to refute this explanation, its force is muted by the outcome of the test with the two control groups that were also tested. During Stage 2, the sphere was a less reliable cue for finding the platform in the two control groups than the two blocking groups and the associative strength of the sphere should therefore have been weaker in the two controls than the two blocking groups. The results shown in Figure 3.6 confirmed this prediction, which demonstrates that the test in the circular pool was at least sufficiently sensitive to detect some between-group differences in the associative strength of the sphere.

As an alternative to a competition between the sphere and the geometric cues for associative strength, it is possible that the present results were a consequence of these cues competing for the attention they are paid. Thus it is conceivable that rats in the blocking groups paid considerably more attention to the sphere after 24 rather than 12 sessions of Stage-1 training. Blocking rats which received only 12 sessions of Stage-1 training would then pay more attention to the geometric cues at the start of Stage 2 than those receiving 24 sessions of pre-training, and thus learn more about the position of the platform with reference to these cues. A benefit of this explanation is that it does not necessarily predict a difference in the associative strength acquired by the landmark in the blocking-12 and blocking-24 groups. It is quite possible that the training in Stage 2 allowed conditioning in both groups with this cue to reach the same asymptote. A further benefit of this attentional explanation is that it does not necessarily predict that the presence of the sphere will overshadow learning about the significance of geometric cues for finding the platform. If extended training is required with the sphere by itself before it distracts attention away from the shape of the environment, then it would follow that overshadowing between these two cues will not be seen if they are presented in compound from the outset of training. It was noted above that in Chapter 2, there was no evidence that the spherical landmark would overshadow spatial learning based on geometric cues provided by a triangular arena.

The results from these experiments lend support to the assertion by Miller and Shettleworth (2007) that previous failures to observe blocking of geometric cues by discrete landmarks were a consequence of inadequate Stage-1 training with the landmark. There is rather less support from the results, however, for the additional assertion of Miller and Shettleworth (2007) that blocking of geometric cues, when it occurs, is due to a competition between the cues for a limited pool of associative strength (e.g. Rescorla & Wagner, 1972). Given the possibility that attentional processes might also have been responsible for the

effects that were reported, it might be a mistake to look to blocking as a tool for assessing whether learning about geometric cues provided by the shape of the environment is governed by a rule such as that advocated by Rescorla & Wagner and the results of Chapter 2 suggest that overshadowing may also be a poor paradigm for assessing cue competition in environments with a distinctive shape. Given the results of Chapter 2 and Chapter 3, alternative tests should be sought whose outcome, if successful, may not be so readily explained in terms of attentional processes. Chapter 4 explored this possibility.

Chapter 4: Conditioned inhibition and superconditioning in an environment with a distinctive shape

4.1. Introduction

As was suggested in Chapter 3, attentional processes may be responsible for blocking in spatial tasks, and this may also explain successful demonstrations of spatial overshadowing. For instance, in the two demonstrations of successful overshadowing of geometric cues by non-geometric cues (Gray et al., 2005; Pearce et al., 2006) where wall colour provided non-geometric information, the rats may concentrate on the wall colour so much that they failed to notice the relevance of the geometric cues for finding the hidden goal. Given such a lack of attention to the geometric cues, it would not be surprising to discover that rather little was learned about them.

It is not easy to see how a choice can be made between an explanation of blocking and overshadowing in terms of competition for associative strength or competition for attention. Accordingly, it may be necessary to seek an alternative methodology in order to test convincingly the proposal that spatial learning based on geometric cues is not governed by the same principles that are believed to apply to associative learning. One possibility is to examine whether training with geometric and non-geometric cues can result in one of them becoming a conditioned inhibitor.

A major success of the Rescorla-Wagner (1972) model is the analysis it offers of conditioned inhibition. If animals receive an A+/AX- discrimination, in which A signals reinforcement and AX signals non-reinforcement, then according to the model A will acquire positive associative strength, and function as a conditioned excitor, while X will acquire negative associative strength and function as a conditioned inhibitor. By virtue of its negative associative strength, X is then predicted to pass both a retardation and summation test for conditioned inhibition (e.g. Rescorla, 1969). For present purposes, an A+/AX-

discrimination is particularly interesting because its solution depends upon an interaction between the effects of conditioning with A and X; X will only acquire inhibition if A is a conditioned excitor. With this in mind, Experiment 1 involved a discrimination in which rats were required to find a submerged platform in one corner of a rectangular pool. This training was then intermixed with trials in which rats were placed in the pool in the absence of the platform, but with a landmark close to where the platform was normally located. According to Rescorla & Wagner (1972), this treatment will result in the geometric cues gaining excitatory associative strength, and the landmark becoming a conditioned inhibitor. If it can be shown that X does indeed acquire inhibitory properties, by passing a summation and retardation test for inhibition, then it would provide strong evidence that learning based on geometric and non-geometric cues is governed by a competitive learning rule such as that proposed by Rescorla and Wagner. Moreover, it is not at all clear how such evidence could be explained by appealing solely to the influence of attentional processes. That is, failing to pay heed, or in contrast, paying attention to X would not necessarily account for X acquiring inhibition. There is already evidence of successful inhibitory conditioning during spatial learning (Sansa, Rodrigo, Santamaria, & Chamizo, in press), but the cues involved were distinct landmarks. It remains to be determined whether a similar effect can be found with geometric cues provided by the shape of the environment.

4.2. Experiment 8

Rats were trained to locate a submerged platform in a grey rectangular-shaped pool (Figure 4.1). Two platforms were used. One platform was located in one corner of the rectangle and the other was located in the diagonally opposite corner (A+ trials). In a subsequent stage rats received discrimination training in which half the trials were A+ trials, as in the previous stage, and for the remaining trials the platforms were removed but identical

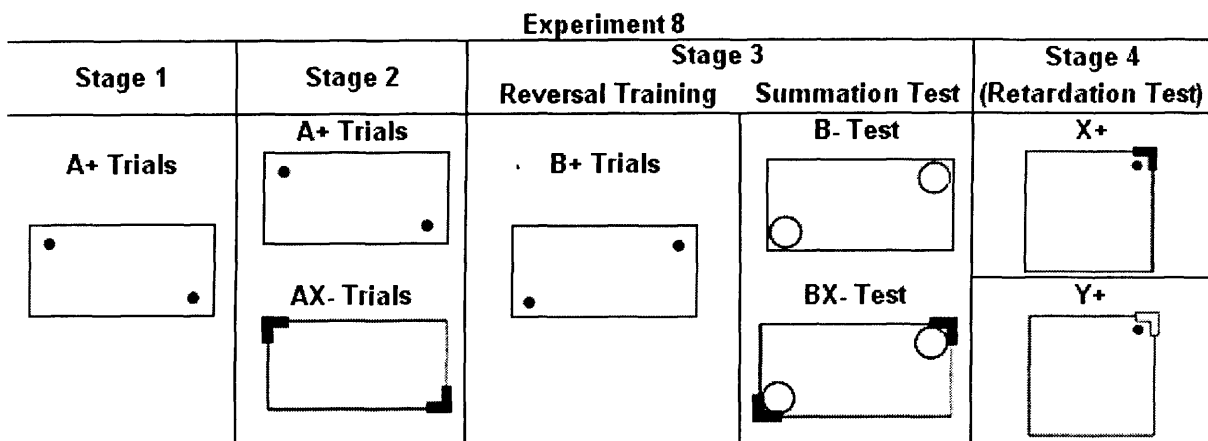


Figure 4.1. Schematic representation of the training stages of Experiment 8. The filled circle represents a submerged platform, black and white 'L' shapes represent landmarks and the open circles represent the 30-cm circular search zones that were used during the analysis of test trials. Only search zones at the correct corners are shown. The walls forming the rectangle and square were grey.

landmarks were located in the two corners where the platforms were normally located (AX-trials). According to Rescorla and Wagner (1972) this discrimination training will result in the landmark acquiring negative associative strength and thus the landmark is predicted to pass both a summation and retardation tests for conditioned inhibition.

A summation test typically involves the conditioned inhibitor being paired with an excitator that is different to the one used for the initial training with the inhibitor. If the previous training has been successful, then the intended inhibitor will weaken the response that is normally elicited by the excitatory test stimulus. In order to provide a novel excitator for a summation test in the present experiment, following the original training, rats were trained with a reversal in which the platforms were moved from the two previously reinforced corners to the previously non-reinforced corners (B+ trials). After completion of this reversal stage, rats were given two test trials. The first trial was in an all grey rectangle in the absence of the platform and landmarks (i.e., B- Test). The second test was in the grey rectangle in the absence of the platform but the intended inhibitory landmarks were present in the corners that were recently established as excitators in the reversal learning stage (BX- Test). If the landmarks acquired negative associative strength, the time spent in the correct corner during the B- test trial should be greater than during the BX- test trial.

A retardation test for inhibition involves pairing the stimulus under scrutiny with the excitatory reinforcer that was used for the initial training. If the stimulus has acquired inhibitory properties then conditioning during the retardation test will progress more slowly than if it is conducted with a neutral stimulus. In the present experiment, a retardation test was conducted by requiring rats to find a submerged platform in one corner of a square pool with a landmark near the platform. For Group X+, the landmark was the same cue that was used for the initial A+/AX- discrimination, and for Group Y+ the landmark was a novel stimulus. If the original training should result in X gaining negative associative strength, then

Group Y+ will learn about the significance of the landmark for finding the platform more readily than Group X+. The walls of both pools were grey, and the landmarks were laminated paper panels that could be attached to the corners of the apparatus. By using black and white panels as the two landmarks, X and Y, it was hoped to minimise generalisation between them.

4.2.1. Method

Subjects and Apparatus. The 32 rats were from the same stock, of approximately the same weight, and housed in the same manner as Experiment 1. All subjects were naïve. The test room and pool were identical to Experiment 1. Two black and two white landmarks were used in this study. Both landmarks consisted of two panels (21 cm X 29.7 cm) that could be attached (via surface tension) to the walls forming a corner in such a way that the longer edges of each panel made contact in the corner of the rectangle.

In Stages 1, 2 and 3, rats were trained in a rectangular-shaped pool constructed from two grey, long Perspex boards (1.8 m long, 0.59 m high, and 2 mm thick) and two grey, short Perspex boards (0.9 m long, 0.59 m high, and 2 mm thick). Each board was placed vertically in the pool and suspended by bars that extended over the edge of the pool. For Stage 4, rats were trained in a square-shaped pool constructed from four, grey boards (1.41 m long, 0.59 m high, and 2 mm thick) made from the same materials as the rectangle.

Procedure. The experiment consisted of four stages (see Figure 4.1). Stages 1, 2 and 3 were conducted in a rectangular pool and Stage 4 was conducted in a square pool. A session was conducted in the same manner as in Experiment 1 except that there were four release points (one on each wall of the rectangle or square). The release point varied across trials with each wall being used once in a given session.

During the 20 sessions of Stage-1 training, a platform was located 25 cm from two of the corners in the rectangle on an imaginary line that bisected the corner. For half of the rats, the platforms were located in the two corners where the short wall was to the left of the long wall. The remaining rats received the platform in the two corners where the short wall was to the right of the long wall (these trials will be referred to as A+ trials). Upon the completion of Stage 1, all rats proceeded to Stage 2 for 10 sessions. Stage 2 was a discrimination phase. Within a session rats received two A+ trials, as in Stage 1. The remaining two trials consisted of training in the rectangle with two landmarks each comprising two panels attached to the walls forming the corners where the platforms were located in Stage 1. For half of the rats the colour of the panels was black and for the remaining rats the panels were white. The platforms were absent from the environment and the rats were allowed to swim in the pool for 60 s before being removed (these trials will be referred to as AX- trials). The order of the different trial types were randomly chosen across sessions. Following the A+/AX- discrimination training, rats proceeded to Stage 3.

Stage 3 was a reversal learning stage which lasted for seven sessions. Rats that received the platforms in the corners where the short wall was to the left of the long wall, now received the platforms in the corners where the short wall was to the right of the long wall. The remaining rats received the converse arrangement (B+ trials). The first three trials of Sessions 5 and 7 were conducted in the manner just described. The fourth trial of these sessions was the summation test. During these test trials, rats were released from the centre of the arena and allowed to swim for 60 s. On the first test trial, half the rats were introduced to the rectangle with the platforms and landmarks absent (B- test). The remaining rats received the same treatment, except that the landmarks used in Stage 2 were present in the new correct corners (BX- test). On the second test, rats that had previously received the B- or the BX-

test received the BX- and B- test respectively. Following the final summation test, rats progressed to the retardation test.

Stage 4, which contained three sessions, constituted the retardation test. For this stage, rats were randomly divided into two groups of equal number ($n = 16$): Group X+ and Group Y+. Group X+ was required to locate a single platform 25 cm from a corner in a square arena on an imaginary line that bisected the corner. Landmark X was attached to the walls of the corner containing the platform. Group Y+ received identical training except that the colour of the landmark was black for those subjects for whom landmark X had been white, and white for those subjects for whom landmark X had been black. At the end of each session, there was a 60-s test trial conducted in the square in the absence of the platform, but in the presence of the landmark.

As for the previous experiments, a record was taken of whether, after being released, a rat entered first, one of the correct corners of the pool – the corners containing the platforms. For the purpose of analysing the results from the test trials in the rectangle, circular search zones were used. Each search zone had a diameter of 30 cm with its centre positioned 25 cm from a corner on a line that bisected the corner. The percentage of time spent in the correct zones (the two where the platforms had been located during training trials) and incorrect zones (the other two corners) of the rectangular pool were analyzed. For the tests trials in the square, the percentage of time spent in a 30-cm diameter circular search zone was also used and its centre was positioned 25 cm from the corner that contained the platform. Any procedural details omitted were identical to Experiment 1.

4.2.2. Results and Discussion

The left-hand panel of Figure 4.2 shows the mean percentage of correct choices across the 20 sessions of training during Stage 1. As can be seen, rats started off slightly above

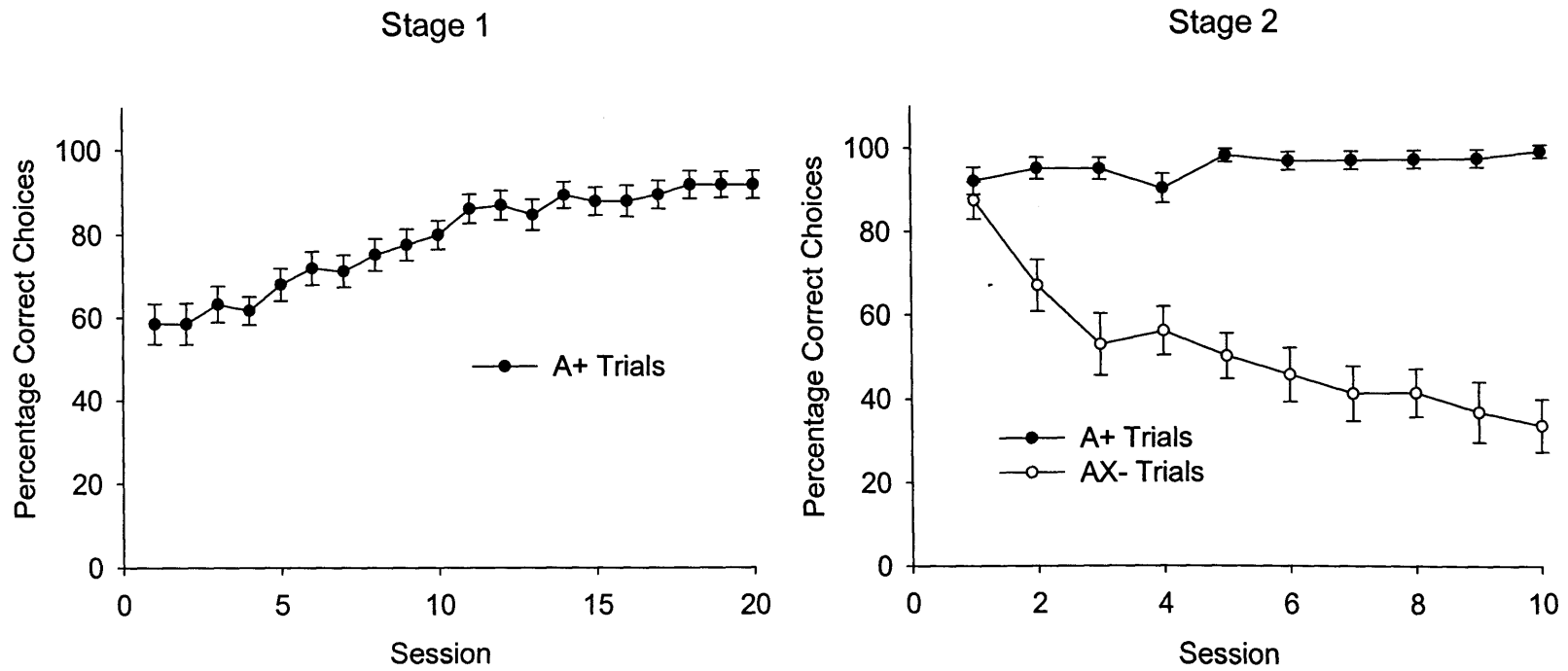


Figure 4.2. Mean (+SEM) percentage of correct choices on A+ trials across Stage 1 (left-hand panel) and on A+ and AX- trials across Stage 2 (right-hand panel) of Experiment 8.

chance, but quickly were making a majority of correct choices towards the end of training. A Wilcoxon matched pairs test conducted on the individual mean percentage of correct choices of the first and last sessions of Stage 1 revealed a significant improvement across Stage 1, $T(24) = 10.0$. The right-hand panel of Figure 4.2 shows the percentage of correct choices for A+ and AX- trials during Stage 2. For the A+ trials, rats made correct choices on virtually every trial, but on AX- trials, rats made progressively fewer correct choices as training progressed. A Wilcoxon matched pairs test was conducted on the individual mean percentages of correct choices combined across sessions and revealed a significant difference between A+ trials and AX- trials, $T(32) = 0$.

The left-hand panel of Figure 4.3 shows the percentage of correct choices across Stage 3. Not surprisingly rats initially headed to the two incorrect corners, which had previously been correct, but then soon relinquished this habit and headed directly for the correct corner on being released into the pool. A Wilcoxon matched pairs test revealed that significantly more correct choices were made by the group during the final than the first session, $T(32) = 0$. The right-hand panel of Figure 4.3 shows the percentage of time spent in the correct and incorrect circular search zones during the summation test. As can be seen, in the absence of landmark X, which had previously signalled the absence of the platform (B-Test) the time spent in the correct zones was far greater than time spent in the incorrect zones. However, in the presence of landmark X (BX- test) there was a slight preference for rats to search in the vicinity of the incorrect corners than the correct corners. A 2 X 2 (Test X Zone) repeated measures ANOVA revealed a significant main effect of test, $F(1, 31) = 36.89$, zone, $F(1, 31) = 16.50$, and a significant Test X Zone interaction, $F(1, 30) = 49.04$. A simple effects analysis on the interaction revealed that during the B- test, rats spent significantly more time in the correct zones than the incorrect zones, $F(1, 62) = 60.71$, but this difference was not significant during the BX- test, $F(1, 62) = 3.85$. Also, during the B- test, rats spent a

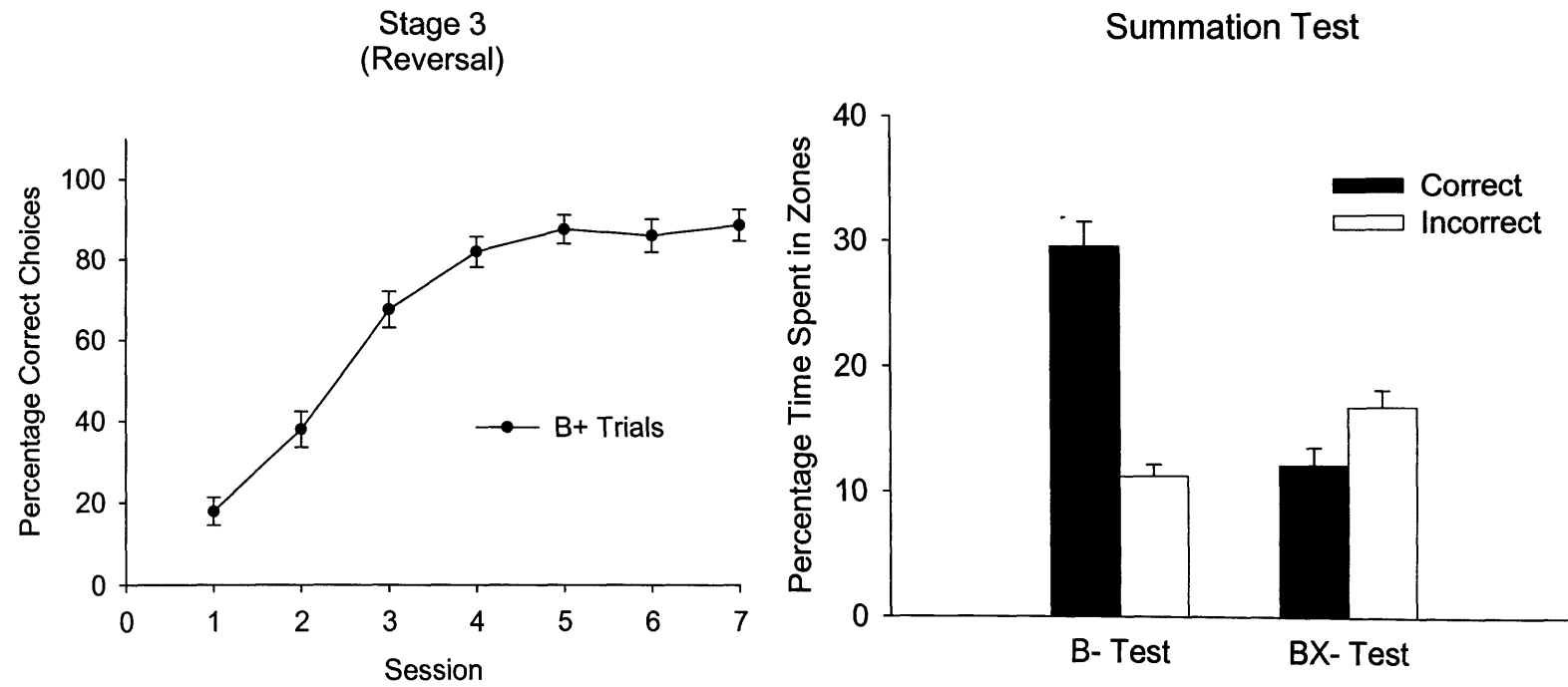


Figure 4.3. Left-hand panel: Mean (+SEM) percentage of correct choices on B+ trials across training in Stage 3 of Experiment 8. Right-hand panel: Mean (+SEM) percentage of time spent in the correct and incorrect zones during the B- and BX- test trials (summation test).

greater proportion of time in the correct zones than during the BX- test, $F(1, 62) = 94.47$, but spent significantly less time in the incorrect zone, $F(1, 62) = 8.88$. These results thus constitute a successful summation test for the inhibitory influence of X.

For the purpose of Stage 4, the rats were randomly assigned to two groups, Group X+ and Group Y+. To ensure the two groups of rats did not differ in any respect in the inhibitory properties of landmark X and the excitatory properties of the geometric cues, a 2 X 2 X 2 (Group X Test X Zone) ANOVA was conducted on the summation test data, where group refers to Groups X+ and Y+; test refers to the B- and BX- test and zone refers to the correct and incorrect zones. None of the effects involving group were significant, $F_s < 1$.

Figure 4.4 shows the mean percentage of correct choices in the square pool in Stage 4; the retardation test. Clearly, rats trained in the presence of landmark X, Group X+, made fewer correct choices across trials compared to Group Y+. A Mann-Whitney U test on the individual mean correct choices combined across the 12 trials for each group revealed that this difference was significant, $U(16, 16) = 6.5$. This result constitutes a successful retardation test for the inhibitory influence of X.

In order to provide a further measure of the rate at which learning about the position of the platform in the square arena took place, the fifth trial of each session of the retardation test consisted of rats being placed in the pool with the landmark but without the platform. It was expected that Group Y+ would spend more time in the corner with the landmark than Group X+. In fact, there was no difference between the groups in this respect. During the three test trials combined, the mean percentage of time spent in the correct corner per trial was 14.49% for Group X+ and 12.83% for Group Y+. This difference was not significant, $t(30) = 1.17$ and thus represents a failure of this aspect of the retardation test to provide evidence of the inhibitory properties of X.

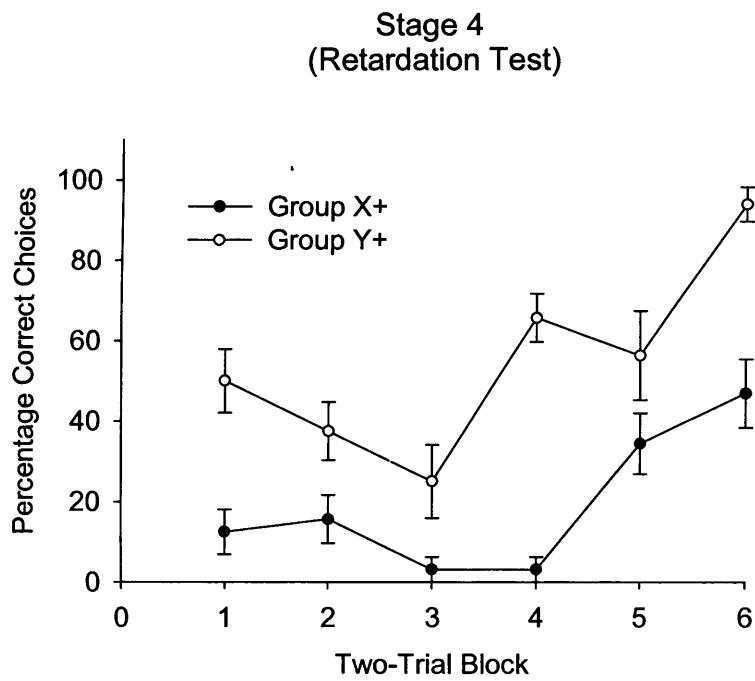


Figure 4.4. Mean (+SEM) percentage of correct choices across Stage-4 training (retardation test) for Group X+ and Group Y+ of Experiment 8.

It is hard to offer with any confidence an explanation for the discrepant outcomes for the two dependent measures of the retardation test. One possibility is that the method on the fifth trial of each session was less sensitive than the method used for the preceding four trials. If this is correct, then the successful summation test, together with the positive outcome from one measure of the retardation test, at the very least lends support to the conclusion that the A+/AX- discrimination training resulted in X becoming a conditioned inhibitor. Before further concluding that the results from these tests therefore endorse the idea that learning about landmarks and geometric cues progresses according to established associative principles (e.g. Rescorla & Wagner, 1972), an alternative explanation for the outcome of the tests needs to be considered.

During the AX- trials of the A+/AX- discrimination, rats would have approached corner A with the expectation of finding an appetitive reinforcer, the platform. According to Amsel and Roussel (1952, see also Amsel, 1992), the omission of an expected appetitive reinforcer can result in frustration. Once aroused, frustration was assumed to be associated with any cues that are present, and result in subjects seeking to avoid those cues in the future. In the case of the present experiment, the A+/AX- discrimination might have resulted in the landmark during Stage 2 being associated with frustration. A tendency to avoid X thereafter would then result in subjects spending less time in the correct corners of the pool when X was present, rather than absent, and thus account for the successful outcome of the summation test. In addition, a tendency to avoid X would also make Group X+ more reluctant than Group Y+ to approach the correct corner in the square and account for the successful outcome of the retardation test. It is thus possible that the results of both tests, although consistent with predictions from the Rescorla-Wagner (1972) theory, were in fact a consequence of a learning process that does not depend upon the cues competing for the associative strength they acquire. Experiments 9a and 9b were conducted in order to address

this possibility by studying whether the A+/AX- discrimination training given in Experiment 8 is capable of resulting in an effect known as superconditioning. We shall see that a successful demonstration of superconditioning in these circumstances is hard to explain by referring to responses that minimise contact with stimuli that are associative with frustration.

4.3. Experiments 9a and 9b

According to the Rescorla-Wagner (1972) theory, the increment in associative strength of a stimulus is determined by the discrepancy between a value set by the magnitude of the reinforcer, and the sum of the associative strengths of all the stimuli present on the trial in question. It then follows that if one of the stimuli is inhibitory the increment in associative strength of a stimulus that accompanies it will be greater than if the inhibitor is absent. Early support for this prediction was provided by Rescorla (1971) and Wagner (1971) who referred to the effect as superconditioning or supernormal conditioning. Another demonstration of superconditioning was provided by Pearce and Redhead (1995) who first trained rats with an appetitive A+/AX- discrimination, before giving them trials in which AX was paired with the same appetitive reinforcer, AX+. Although A can be expected to have high associative strength at the end of discrimination training, the presence of X during the AX+ trials will provide the opportunity for further increments in the associative strength of A. As a consequence, it follows from the Rescorla-Wagner (1972) theory that the associative strength of A will ultimately be greater than if the additional conditioning with A does not take place in the presence of X. This prediction was confirmed by Pearce and Redhead.

From the point of view of the present discussion, superconditioning is important because it is hard to explain why it should occur by referring to the influence of responses elicited by frustration. In the case of the experiment by Pearce and Redhead (1995), for example, if X elicited frustration as a consequence of the A+/AX- discrimination, then it is

not clear why responses directed at minimising contact with X should facilitate conditioning with A during the AX+ trials. It would thus appear that superconditioning provides a particularly good test of whether or not learning about two or more stimuli when presented together is governed by a competitive learning rule such as that embodied in the Rescorla-Wagner (1972) theory. With this in mind, the next two experiments examined if it is possible to observe superconditioning between a landmark and a geometric cue. The experiments were based on the design of Pearce and Redhead and used the A+/AX- discrimination employed in Experiment 8.

The training for Experiment 9a took place in a rectangular pool. Rats were randomly divided into a superconditioning and a control group. Both groups received Stages 1 and 2 training, A+ followed by A+/AX-, as in Experiment 1 (see Figure 4.5). This initial training was intended to result in the geometric cue at the correct corners becoming a conditioned excitator and the landmarks becoming a conditioned inhibitor. In order to determine if the training had been successful in this respect, test trials were given towards the end of Stage 2 in the presence and the absence of X, with the platforms removed from the pool. It was anticipated that both groups would spend more time in the correct corners of the rectangle in the absence than the presence of X.

In the following stage, the superconditioning group was trained in a rectangle to locate a platform located in the same corners as in the previous stages but landmark X was also present in these corners, AX+ trials. The control group received the same training except the landmark was a novel colour, AY+ trials. If landmark X acquired negative associative strength resulting from the A+/AX- discrimination in Stage 2 then, according to Rescorla and Wagner (1972), subsequent AX+ trials will result in additional excitatory learning to both landmark X and the geometric cue, A. For the control group, the neutral associative strength of Y will lead to excitatory learning with both A and Y being slight.

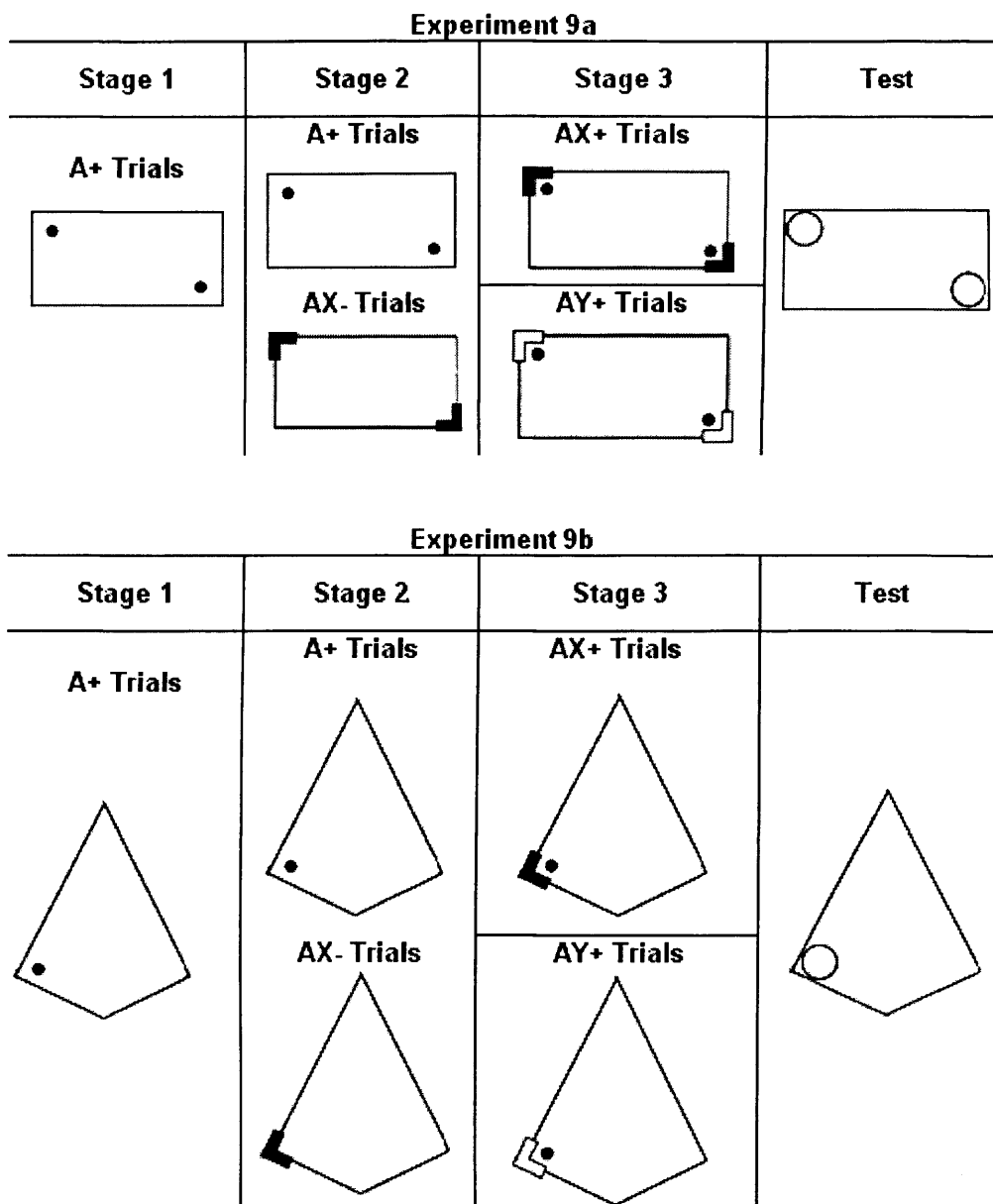


Figure 4.5. Schematic representation of the training stages of Experiments 9a and 9b. The filled circle represents a submerged platform, black and white 'L' shapes represent landmarks and the open circles represent the 30-cm circular search zones that were used during the analysis of test trials. Only search zones at the correct corners are shown. The walls forming the rectangle and kite were grey.

A test in the rectangle in the absence of the landmarks and platform should then result in the superconditioning group spending a greater proportion of time in the corner where the platform would normally be located than the control group.

Experiment 9b was conducted in the same manner as Experiment 9a, except all training took place in a kite-shaped pool and it commenced after the completion of Experiment 9a with new groups of rats. In addition to confirming the generality and the reliability of the results from Experiment 9a, there was a further reason for conducting Experiment 9b. Past research has shown that blocking and overshadowing of geometric cues occur in the rectangle when two adjacent walls forming the rectangle are black and the remaining two walls are white (Pearce et al., 2006). A similar experiment conducted in the kite showed evidence of potentiation rather than cue competition (Graham et al., 2006; Pearce et al., 2006). There is no clear explanation for why the colour of the walls should potentiate learning about geometric cues in some environments, and disrupt such learning in others, but given this pattern of results, superconditioning might not be expected in the kite as learning about this shape does not appear to be governed by a competitive learning rule. However, if superconditioning can be demonstrated in the kite, then this would provide the first empirical demonstration in animals that learning about geometric cues in this environment obeys the principles of associative learning.

4.3.1. Method

Subjects. Experiments 9a and 9b each contained 32 rats from the same stock, of approximately the same weight, and housed in the same manner as for Experiment 8. The rats for Experiment 9a had not participated in a previous experiment whereas those for Experiment 9b had been previously used in an appetitive conditioning.

Apparatus. The apparatus and landmarks for Experiment 9a were the same as for Experiment 8, except the square arena was not used. The apparatus for Experiment 9b was the same as for Experiment 9a, except the boards forming the rectangle now formed a kite-shaped pool with one right-angled corner with a short wall to the left of a long wall, and another right-angled corner with a short wall to the right of a long wall. Only one platform was needed in this experiment as there was only one correct corner.

Procedure. Rats in Experiment 9a were randomly assigned to a superconditioning and a control group in equal numbers ($n = 16$). Both groups received identical training in Stages 1 and 2, which were conducted in the same manner as in Experiment 8 except that Stage 2 consisted of 14 sessions. In Session 10 and 12 of Stage 2, the first three trials were conducted in the same manner as previous trials. The fourth trial of these sessions was either an A- test trial or an AX- test trial conducted in the same way as the summation test in Experiment 8. Half the rats received the test with A- in Session 10, and with AX- in Session 12. The remaining rats received the converse arrangement. After the test trials, the rats received an additional two sessions of Stage-2 training before progressing to Stage 3.

For the five sessions of Stage 3 the two platforms were located in the same corners as for the previous stage, and a landmark consisting of two panels was attached to the walls in each of the correct corners. The colour of the panels was the same as for the previous stage for the superconditioning group, and opposite to that of Stage 2 for the control group. Any procedural details omitted were the same as for Experiment 8.

The procedure for Experiment 9b was identical to Experiment 9a except that training took place in a kite-shaped pool. For half of the rats in each group, the correct corner was the right-angled corner where the short wall was to the left of the long wall and for the remaining rats the opposite corner was the correct corner. All other procedural details including the

number of sessions per stage, and the manner in which the training and test trials were conducted, were identical to Experiment 9a.

4.3.2. Results and Discussion

Figure 4.6 shows the mean percentage of correct choices for both groups throughout training in Stage 1 in the rectangle (left-hand panel) and the kite (right-hand panel). In both environments, the superconditioning and control groups started off close to chance (50% in the rectangle, 25% in the kite) and then gradually made correct choices on virtually every trial by the end of training. Separate statistical analyses were carried out for the results from the two environments. Mann-Whitney U tests were conducted on the individual mean percentage of correct choices combined across the last three sessions for each group and revealed no difference between the two groups trained in the rectangle, $U(16, 16) = 122.5$, and in the kite, $U(16, 16) = 110$.

Figure 4.7 shows the percentage of corrects choices on A+ and AX- trials for the superconditioning and control groups throughout Stage 2 in the rectangle (left-hand panel) and the kite (right-hand panel). In both the rectangle and the kite the same pattern of results emerged. During A+ trials, the majority of the rats' first choices were to the correct corner. On AX- trials, rats in both groups gradually made fewer correct choices as training progressed. For Experiment 9a in the rectangle, a Wilcoxon matched pairs test was conducted on the mean percentage of correct choices combined across the last three sessions for the superconditioning and control groups. This analysis revealed that for both groups, rats made more correct choices during A+ trials than AX- trials, $T_s = 0$. Also, a Mann-Whitney U tests conducted on the mean percentage correct choices combined across the last three sessions revealed no significant differences between the groups on A+ trials, $U(16, 16) = 128$ or on AX- trials $U(16, 16) = 121.5$. An identical analysis for Experiment 9b in the kite

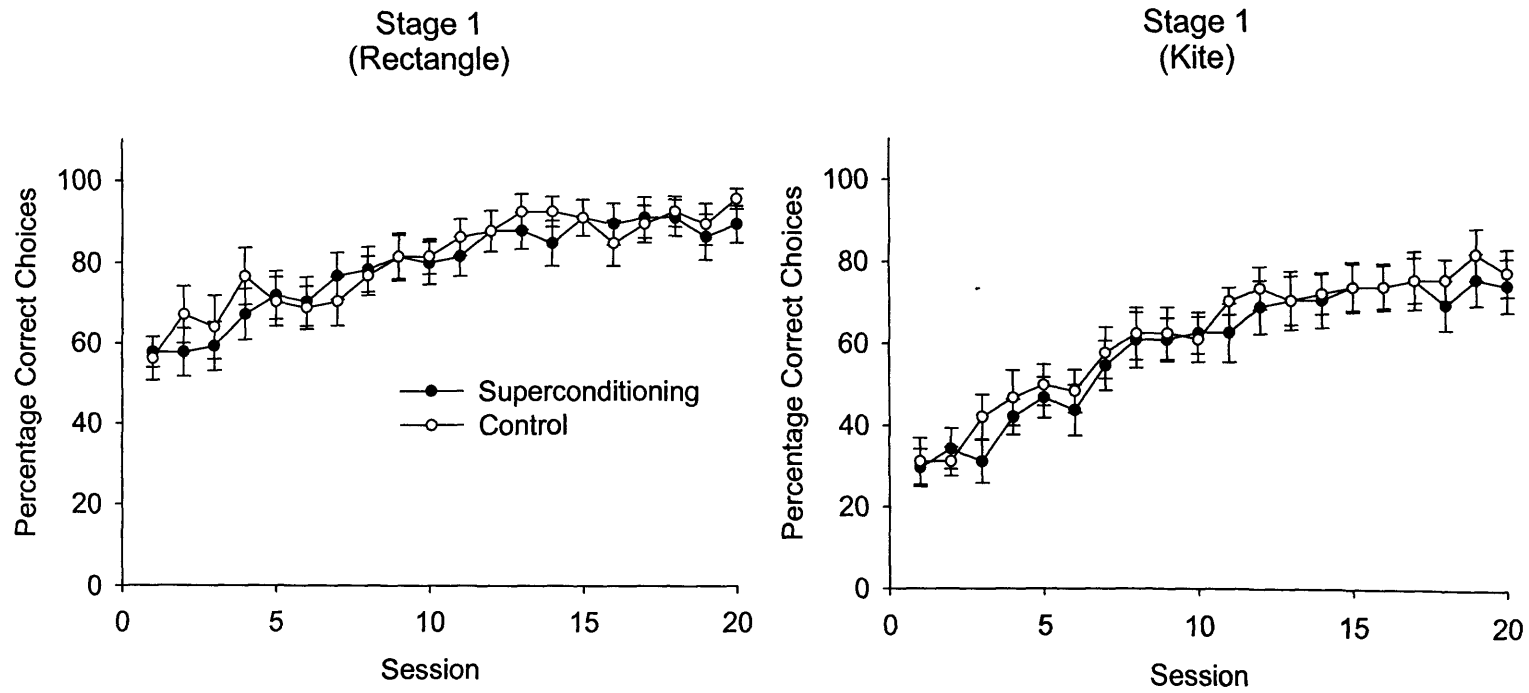


Figure 4.6. Mean (+SEM) percentage of correct choices across Stage-1 training for the superconditioning and control groups of Experiment 9a (left-hand panel) and Experiment 9b (right-hand panel).

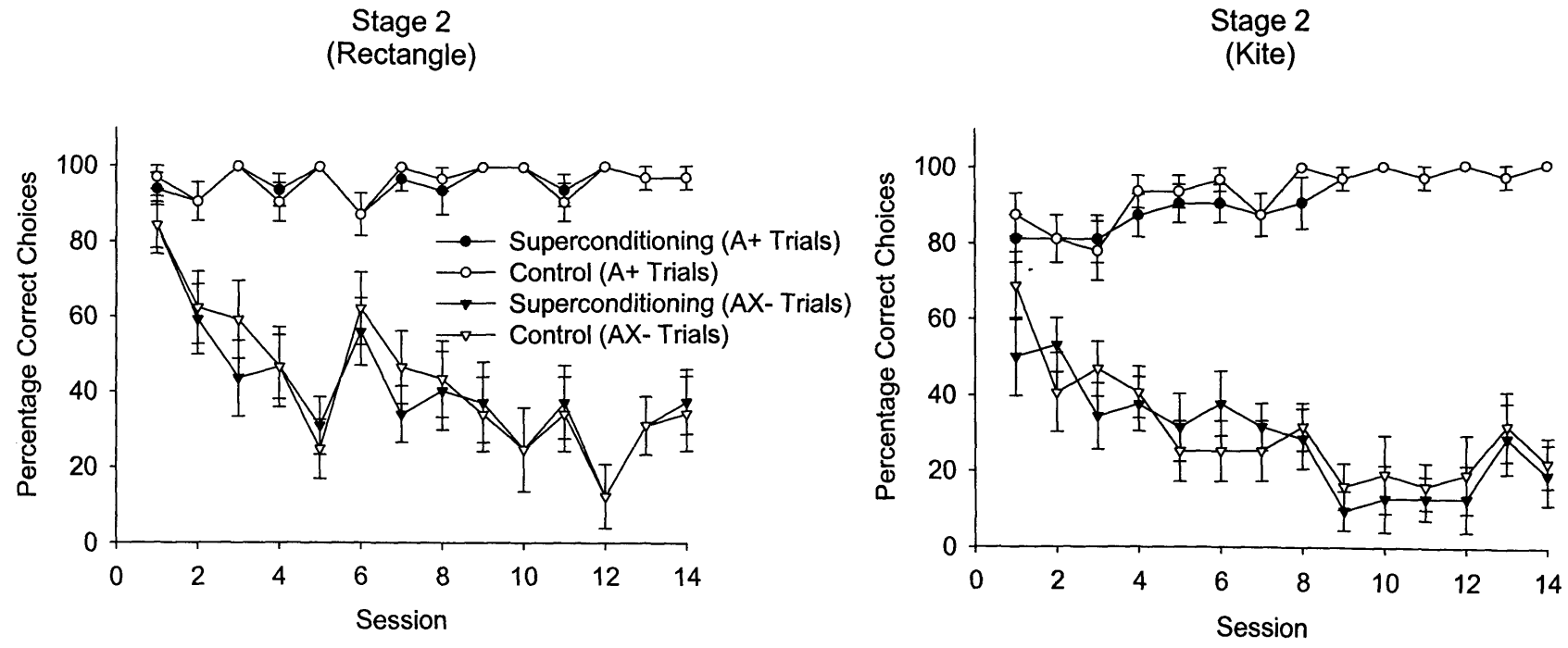


Figure 4.7. Mean (+SEM) percentage of correct choices on A+ and AX- trials across training in Stage 2 for the superconditioning and control groups of Experiment 9a (left-hand panel) and Experiment 9b (right-hand panel).

revealed similar results. During the final three sessions of this stage, rats in both the superconditioning and control groups made more correct choices during A+ trials than AX- trials, $T_s = 0$ and there was no difference between the two groups on A+ trials, $U(16, 16) = 128$ or on AX- trials $U(16, 16) = 117$.

Figure 4.8 shows the time spent in the correct zones during the A- and AX- test trials in the rectangle (left-hand panel) and in the kite (right-hand panel). In both environments, the superconditioning and control groups spent a greater proportion of time in the correct zones during the A- test than the AX- test. This outcome is consistent with the claim that X had acquired inhibitory properties. For the test trials conducted in the rectangle, a 2 X 2 (Group X Test) ANOVA revealed a significant test effect, $F(1, 30) = 38.47$. The group effect and the Group X Test interaction were not significant, $F_s < 1$. An identical analysis on the time spent in the correct zone for the two test trials in the kite revealed a significant test effect, $F(1, 30) = 61.85$. The group effect and the Group X Test interaction were not significant, $F_s < 1$.

Figure 4.9 shows the percentage of correct choices for Stage 3 in the rectangle (left-hand panel) and the kite (right-hand panel) where the superconditioning and control groups received AX+ and AY+ training respectively. In both environments, the superconditioning group initially made incorrect choices but by the end of training, there was no difference between the groups. The lack of difference between the groups was confirmed by Mann-Whitney U tests conducted on individual mean percentages of correct choices combined across the last three sessions in the rectangle, $U(16, 16) = 112.5$, and in the kite, $U(16, 16) = 104$

The most important results from the experiment concern the outcome of the test in the empty arena at the end of Stage 3. In order to determine whether the AX+ training during Stage 3 for the superconditioning group augmented responding to A, the results from the final

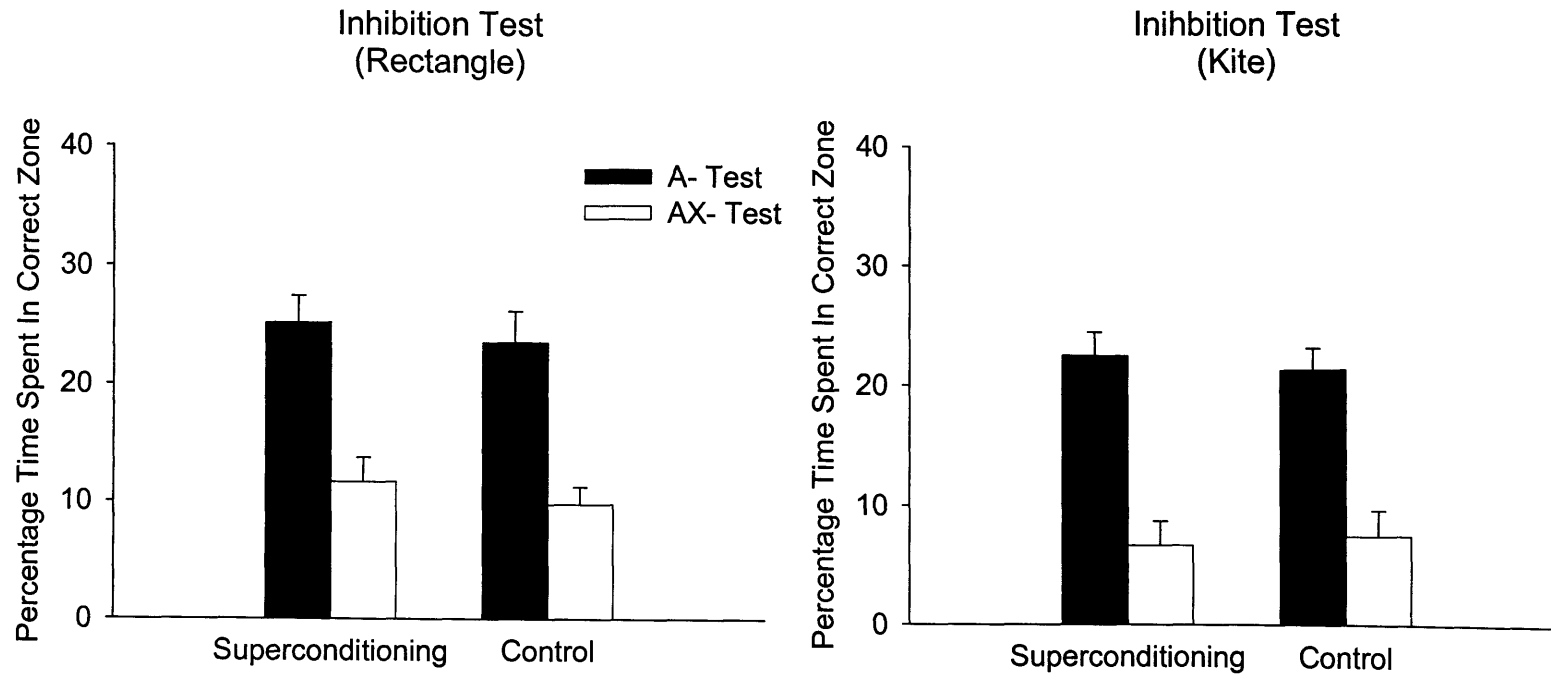


Figure 4.8. Mean (+SEM) percentage of time spent in the correct zone during the A- and AX- test trials for the superconditioning and control groups of Experiment 9a (left-hand panel) and Experiment 9b (right-hand panel).

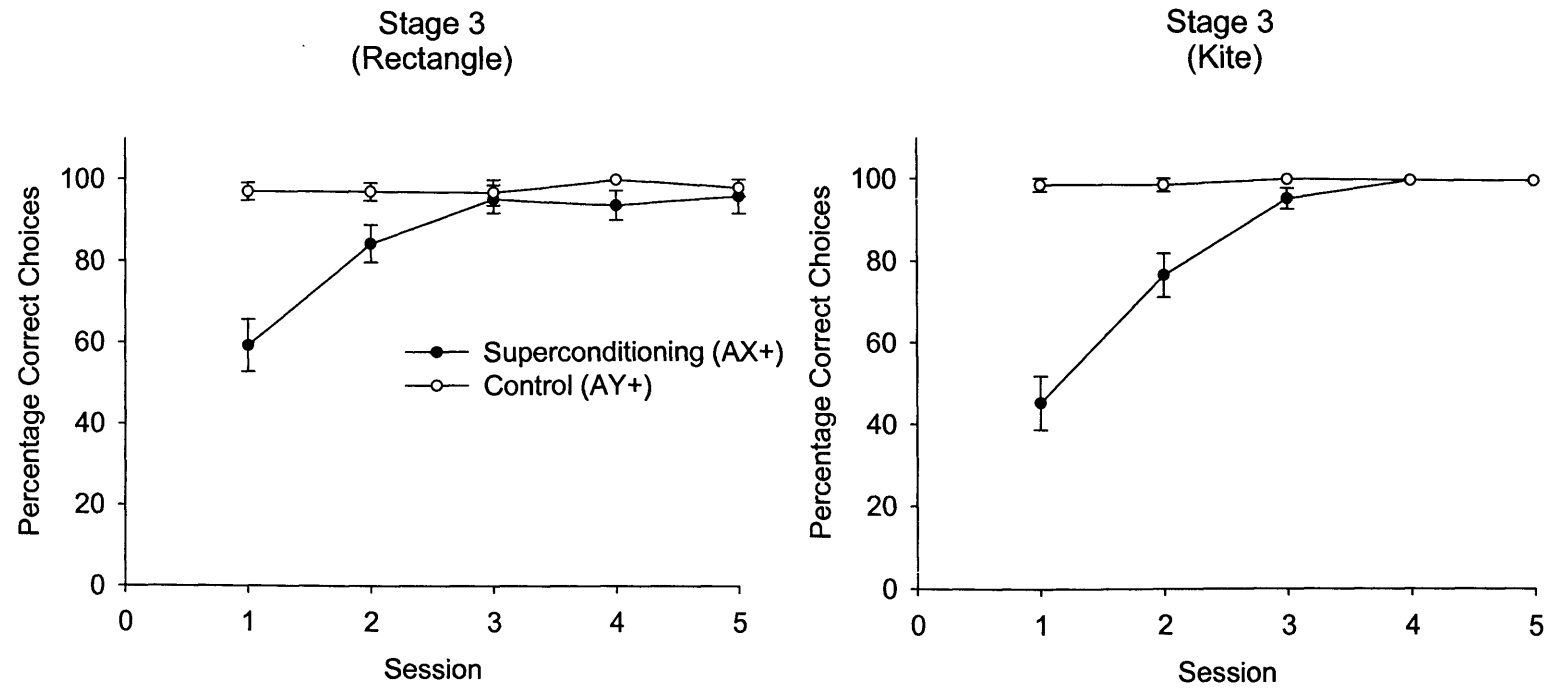


Figure 4.9. Mean (+SEM) percentage of correct choices for the superconditioning and control groups across Stage-3 training of Experiment 9a (left-hand panel) and Experiment 9b (right-hand panel).

test trial can be compared with the equivalent results for the control group, and with the results from the A- test trial that took place just before the start of Stage 3. Both results are shown in Figure 4.10, where the filled histograms depict the mean time spent by each group in the correct search zones during the A- test before Stage 3. These results thus correspond to the filled histograms in Figure 4.8. The open histograms in Figure 4.10 depict the results from the A- test trial for the superconditioning group at the end of Stage 3. From the left-hand panel of Figure 4.10, it is evident that the superconditioning group of Experiment 9a spent more time in the correct search zones in the rectangle during the test trial after Stage 3, either than during the test trial before Stage 3, or than the control group during the final test trial. In addition, there was no indication of a similar increase in performance between the two test trials for the control group. The foregoing observations were supported by the outcome of a 2 X 2 (Group X Test) ANOVA conducted on the percentage of time spent in the correct zone for the test trial before and after Stage 3. This analysis revealed a significant test effect, $F(1, 30) = 4.57$, and a significant Group X Test interaction, $F(1, 30) = 5.46$. The main effect of group was not significant, $F(1, 30) = 3.84$. A simple effect analysis on the interaction revealed the time spent in the correct zones during the test trial after Stage 3 was greater than the test trial before Stage 3 in the superconditioning group, $F(1, 30) = 10.02$, but not in the control group, $F < 1$. Also, the time spent in the correct zones during the test trial before Stage 3 was similar between the two groups, $F < 1$, but the time spent in the correct zones during the test trial after Stage 3 was greater in the superconditioning group compared to the control group, $F(1, 60) = 8.20$.

These results thus imply that the AX+ trials for the superconditioning group enhanced the control over searching for the platform by the geometric cues relative to that seen prior to Stage 3, and relative to that seen in the control group. In other words, the results demonstrate

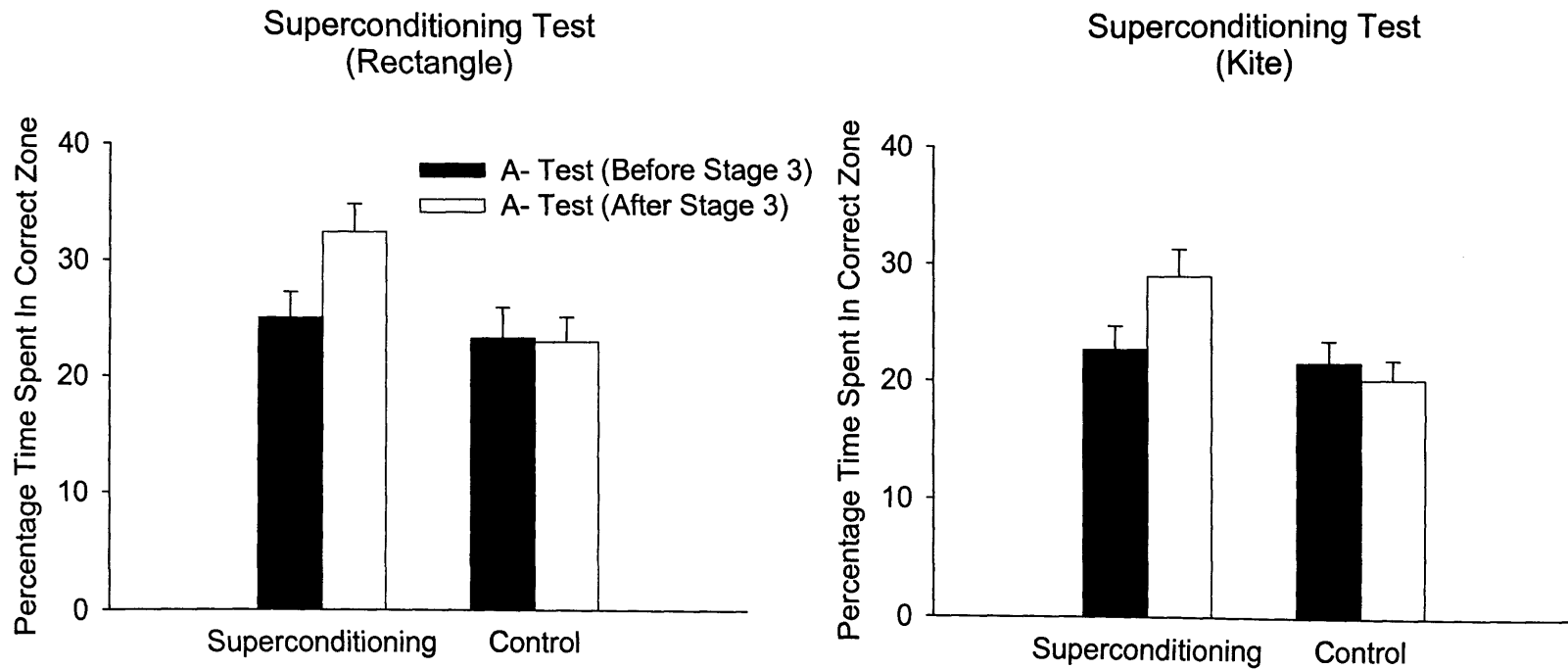


Figure 4.10. Mean (+SEM) percentage of time spent in the correct zone during the A- test trial conducted before and after Stage-3 training for the superconditioning and control groups of Experiment 9a (left-hand panel) and Experiment 9b (right-hand panel).

that the AX+ trials resulted in superconditioning with the geometric cues provided by the rectangle.

The right-hand panel of Figure 4.10 shows that the outcome of the test trials in Experiment 9b was remarkably similar to that in Experiment 9a. A 2 X2 (Group X Test) ANOVA revealed a main effect of group, $F(1, 30) = 4.17$, and a significant Group X Test interaction, $F(1, 30) = 10.38$. The effect of test was non-significant, $F(1, 30) = 3.99$. A simple effects analysis on the interaction revealed a significant preference for the correct zone during the test after Stage 3, than before Stage 3 in the superconditioning group, $F(1, 30) = 13.62$, but not in the control group, $F < 1$. Time spent in the correct zones during the test after Stage 3 was significant between the superconditioning and control groups, $F(1, 60) = 10.48$, but not during the test before Stage 3, $F < 1$.

Experiments 9a and 9b demonstrate that the presence of a landmark, which had previously signalled the absence of the platform, augmented learning about geometric cues when it was situated near the platform in one corner of either a rectangular or a kite-shaped pool. These results are in keeping with the claim that learning about geometric and non-geometric cues are governed by the same competitive learning rule that appears to apply to other sorts of learning such as Pavlovian conditioning (e.g. Rescorla & Wagner, 1972). Although there is some evidence to support this conclusion from experiments in a rectangular arena (e.g. Gray et al., 2006; Pearce et al., 2006) and a triangular arena (See Chapter 3), this is the first occasion that support for this conclusion has been found using the geometric cues provided by a kite-shaped arena.

One prediction that follows from the Rescorla-Wagner (1972) rule, see also Pearce (1994) is that not only will superconditioning occur with an excitator when it is paired with an inhibitor for conditioning, but the additional learning with the excitator may surpass asymptote. The experimental design used in the present experiments allows one to comment on this

prediction. In each experiment, the control group spent a similar amount of time in the correct part of the pool during the test trials that took place immediately before and after Stage 3. It thus seems likely that the associative strength acquired by the geometric cues was at asymptote after the A+/AX- discrimination training in Stage 2. If this line of reasoning is applied to the superconditioning groups, then the strength of the response elicited by the geometric cues during the test at the end of Stage 3 must have been greater than asymptotic. That is, it was stronger than would be expected if training had taken place entirely in the absence of the landmark. The results therefore provide support for those theories that predict superconditioning can result in a greater than asymptotic level of responding to the stimulus paired with an inhibitor (e.g. Pearce, 1994; Rescorla & Wagner, 1972).

The results from Experiments 9a and 9b are hard to explain if it is assumed that the A+/AX- discrimination training was effective because it resulted in rats learning to avoid or withdraw from the landmark. Although this assumption is able to account for the results from Experiment 8, it is not at all obvious how being required to reverse this tendency during the AX+ trials in the superconditioning group should enhance the control acquired by the geometric cues relative to the control group.

4.4. Summary and Conclusions

In three experiments rats were first trained with a spatial A+/AX- discrimination in which a submerged platform could be found in one corner of a pool with a distinctive shape when a landmark was absent, but not when it was present in the same corner. Experiment 8 revealed that the landmark passed a summation test, and one of two retardation tests for inhibition. Experiments 9a and 9b revealed that the properties acquired by the landmark during the discrimination training enabled it to promote superconditioning with the geometric cues when rats were subsequently required to find the platform near these cues in the

presence of the landmark. These results provide the first demonstration of superconditioning in a spatial task and strongly suggest the landmark acquired inhibitory properties, as envisaged by Rescorla and Wagner (1972), as a result of the discrimination training.

An important reason for conducting the present experiments was to determine if a competitive learning rule, which appears to govern such forms of associative learning as Pavlovian conditioning, also applies to the interaction between geometric and non-geometric cues during spatial learning. The results from the reported experiments strongly suggest that a competitive learning rule does indeed apply to learning based on geometric and non-geometric cues. We noted that the results of Chapter 3 and the two instances of overshadowing of geometric cues (Gray et al., 2005; Pearce et al., 2006) also suggest that this rule applies to the interaction between these cues, but those results are ambiguous because they may have been a consequence of a competition for attention rather than associative strength. Is it possible that the outcome of the present experiments can also be interpreted by appealing to selective attentional processes (e.g., Sutherland & Mackintosh, 1971)? Given the ambiguity that already surrounds the interpretation of the results from Experiment 8 because its outcome might have been affected by responses seeking to alleviate frustration, I shall concentrate on Experiments 9a and 9b. In fact, it seems most unlikely that an appeal to attentional processes can provide a satisfactory account for the results from these experiments. At the start of Stage 3, both groups in each experiment can be expected to pay the same amount of attention to A, because their training with this stimulus had been identical up to this point. To explain the superior performance with A in the superconditioning than the control group at the end of this stage, it would then have to be assumed that Y distracted attention away from A in the control group to a greater extent than X in the superconditioning group. However, since Y was initially neutral, and X can be assumed to be inhibitory at the outset of Stage 3, it seems likely that more attention would be paid to X than Y during this

stage and result in weaker conditioning with A in the superconditioning than the control group. In support of this conclusion, it is interesting to note that the introduction of the novel landmark to the control group at the outset of Stage 3 did not disrupt at all the control acquired by the geometric cues. Such a finding supports the claim that rats paid little heed to this stimulus. Furthermore, if it is accepted that the training in Stage 3 resulted in A acquiring greater than asymptotic associative strength, then it is not easy to explain this outcome by referring solely to attentional processes.

Up until now, superconditioning has been explained in terms of the elemental model of Rescorla and Wagner (1972). However, the configural theory of Pearce (1987) contains a similar error-correction rule to that proposed by Rescorla and Wagner, and the theory may thus be of some relevance to the present results. According to Pearce, responding to a pattern of stimulation is governed by its own excitatory strength and any other that generalises to it due to conditioning with similar patterns. In the case of the present experiment, the A+/AX-discrimination stage would initially result in A gaining excitatory strength which would generalise to AX. To counter this excitation, AX must enter into an inhibitory association which will generalise to A. With sufficient gains in excitatory strength to A, and inhibitory strength to AX, the former will possess net positive associative strength of asymptotic value, and the overall associative strength of the latter will be zero. Conditioning with AX during Stage 3 will leave it with positive associative strength and enhance responding to A through generalisation. Thus the theory is able to predict the superconditioning that was observed. The training for the control group will result in AY acquiring excitatory strength which should also enhance responding to A through generalisation. However, there will be less scope for excitatory conditioning with AY than AX, because when AY is first introduced generalisation from A will ensure it has more associative strength than AX. The theory therefore correctly predicts that the final test with A will reveal a stronger response in the

superconditioning than the control group. However, the additional prediction from the theory that superconditioning should have been recorded in the control group was not confirmed. It is possible that our method of testing was not sufficiently sensitive to detect superconditioning in the control group. Alternatively, as Pearce and Redhead (1999) have proposed, superconditioning after the training given to the control group, may be possible only when A and AY signal different reinforcers of the same affective value.

By supporting predictions derived from the Rescorla-Wagner (1972) theory, the present results, at first glance seem to endorse the associative model of spatial learning put forward by Miller and Shettleworth (2007). However a simulation of Experiment 9a was conducted using Equations 1.3 and 1.4 (p. 35) and with the same parameters as they suggest and it appears that the model fails to predict superconditioning. Figure 4.11 shows a simulation based on Miller and Shettleworth's model that shows the probability of choosing the correct corner across trials for the three stages of the experiment. As can be seen, the model accurately predicts the acquisition functions obtained in Stages 1, 2 and 3 of Experiment 9a (c.f., Figures 4.6, 4.7 & 4.9). The problem arises when calculating the probability of choosing the correct corner during tests in the absence of the landmark at the end of Stage 2 and Stage 3 training. Figure 4.12, shows the simulated results for a test trial in the absence of the landmark for the control and superconditioning groups before and after Stage-3 training. Miller and Shettleworth's model predicts a greater probability of choosing the correct corner prior to Stage 3 training for the superconditioning group, inconsistent with the results of Experiment 9a (c.f., Figure 4.10).

To determine why Miller and Shettleworth's (2007) model fails to explain superconditioning, one needs to look at the associative strengths of each element predicted by the model. Figure 4.13 shows the cumulative associative strength of the geometric cues of the correct and incorrect corners, G_C and G_I respectively, the common cue, B, and the

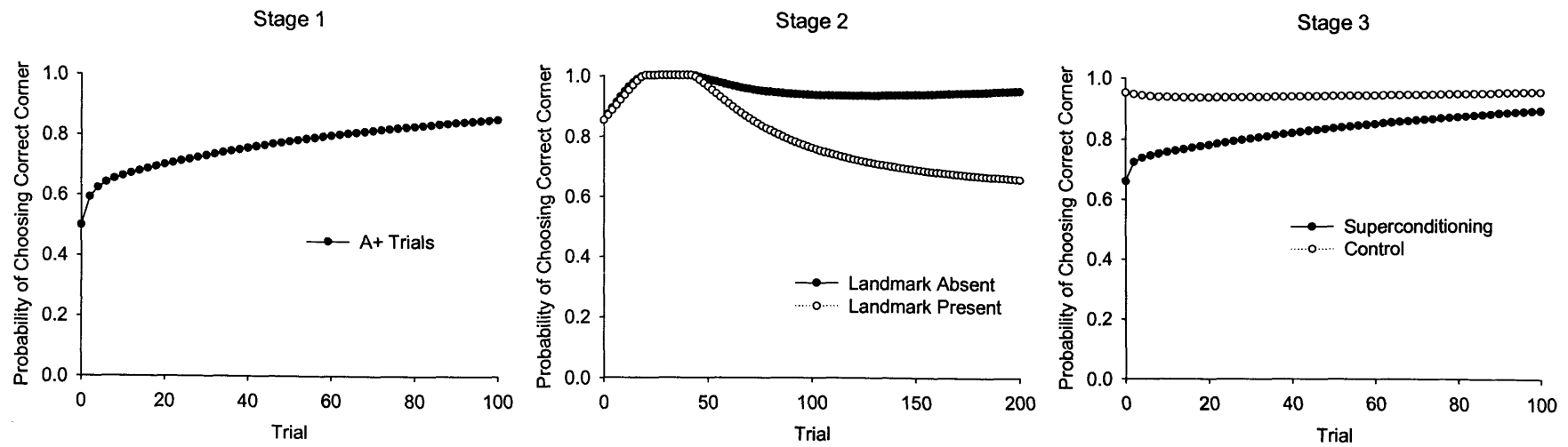


Figure 4.11. Simulated training data based on Miller and Shettleworth's (2007) model of learning about geometric cues for Experiment 9a. It shows the probability of choosing the correct corner in the presence of all the elements presented throughout training during Stages 1 (left-hand panel), 2 (centre panel), and 3 (right-hand panel).

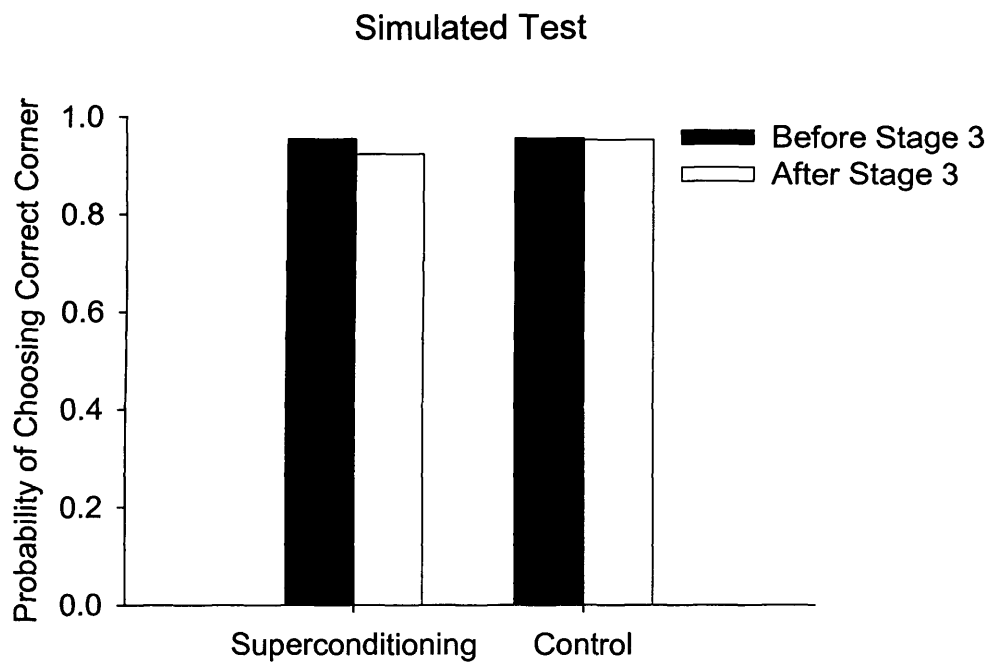


Figure 4.12. Simulated results of Experiment 9a based on Miller and Shettleworth's (2007) model of learning about geometric cues. Black histograms refer to the probability of choosing the correct corner in the absence of any landmarks before the commencement of Stage 3. The white histograms refer to the probability of choosing the correct corner in the absence of any landmarks after the completion of Stage 3.

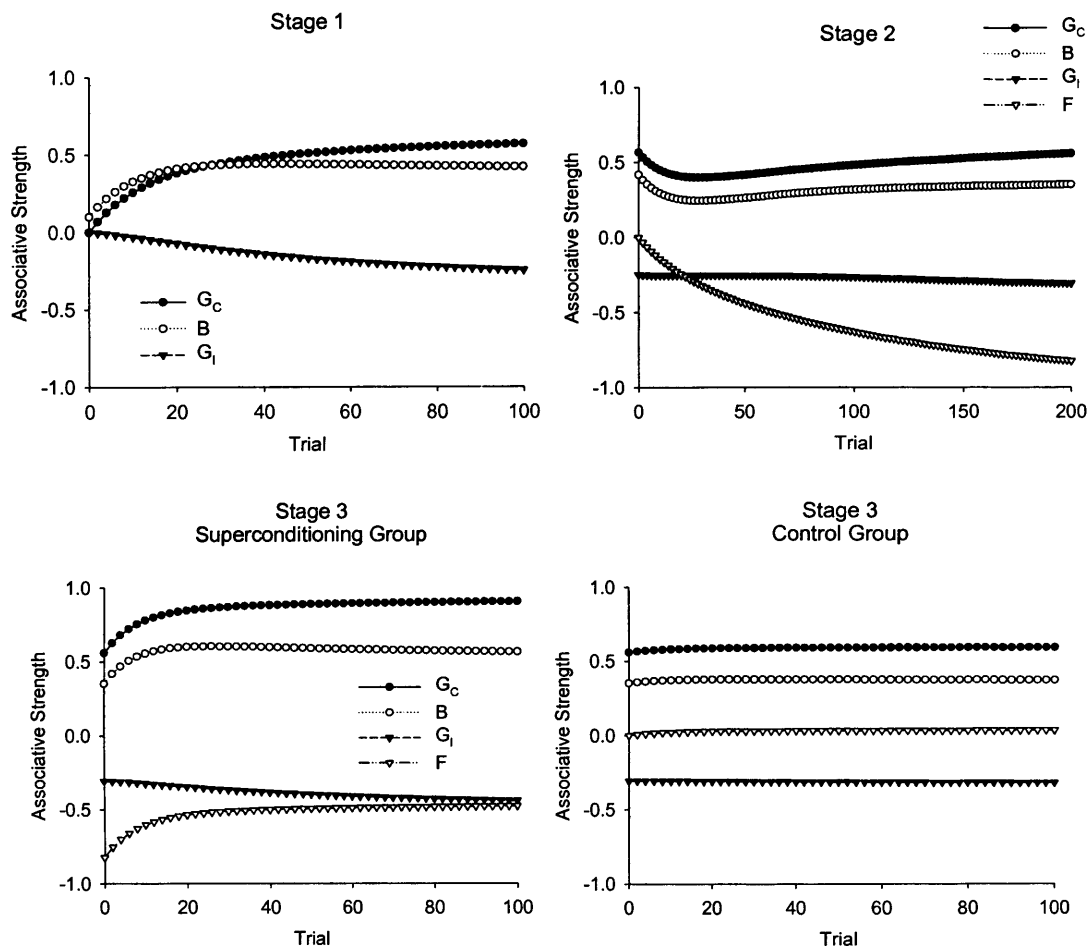


Figure 4.13. The results from computer simulations of Experiment 9a based on the associative model of geometry learning by Miller and Shettleworth (2007). Top row: The predicted acquisition of associative strength by all of the cues in the rectangle for Stage 1 (left-hand panel) and Stage 2 (right-hand panel). Bottom row: The predicted acquisition of associative strength by all of the cues in the rectangle for Stage 3 for the superconditioning (right-hand panel) and control (left-hand panel) groups. G_c , G_I = the geometric cues at the correct, and incorrect corners. F = the landmark, B = the common cue. Note that the landmark in Stage 3 for the control group is a novel landmark that has an initial associative strength of zero.

landmark, F, across each stage of the experiment. In the first stage, animals received A+ trials. As it is shown in the top-left hand panel of Figure 4.13, G_C and B increase in associative strength because the platform is located in the correct corners, while G_I gains negative associative strength across training because no platform is ever presented in the incorrect corners. During Stage 2 when the A+/AX- discrimination is introduced (see top right-hand panel of Figure 4.13), G_C and B continue to gain modest amounts of associative strength, G_I continues to gain minimal negative associative strength, but F, the intended inhibitory landmark, gains a substantial amount of negative associative strength because the landmark is present in the correct corners during non-reinforced trials. At this point the superconditioning and control groups do not differ with respect to their training.

In the third stage, the superconditioning group receives AX+ trials while the control group receives AY+ trials. The landmark, F in the simulation for the superconditioning group refers to the inhibitory landmark used in Stage 2, but for the control groups, F refers to a neutral landmark with an initial associative strength of zero. As can be seen in the bottom row of Figure 4.13 the associative strength of G_C in the superconditioning group is considerable larger compared to the control group at the end of Stage-3 training. One might assume this abnormally high associative strength of G_C in the superconditioning group compared to the control group would result in performance during a test trial being better in the superconditioning group than the control group, but Miller and Shettleworth's (2007) model uses Equation 1.2 (p. 35) to calculate the probability of choosing the correct corner during a test, in the absence of the landmark. In the worked example shown below, after 100 trials of Stage-3 training, Miller and Shettleworth's choice rule is implemented for Experiment 9a where P_C is the probability of choosing the correct corner. V_C , and V_I are the total associative strength of the elements at the correct and incorrect corners respectively. G_C and G_I are the associative strengths of the geometric cue at the correct and incorrect corners

respectively and B is the associative strength of the common cue. F is omitted from the equation because it is absent on the test trial at the end of Stage 3.

$$P_C = \frac{V_C}{V_C + V_I} \quad (\text{Worked Example})$$

$$P_C = \frac{G_C + B}{(G_C + B) + (G_I + B)}$$

Superconditioning Group

$$P_C = \frac{.91 + .57}{(.91 + .57) + (-.44 + .57)}$$

$$P_C = \frac{1.48}{1.61} = .92$$

Control Group

$$P_C = \frac{.59 + .37}{(.59 + .37) + (-.32 + .37)}$$

$$P_C = \frac{.96}{1.01} = .95$$

Given this equation, the relative higher associative strengths of G_C and B in the superconditioning group results in the denominator being relatively greater than the numerator in the superconditioning group than in the control group and thus results in a lower probability of choosing the correct corner.

Miller and Shettleworth's (2007) model does an adequate job describing the accumulation of associative strength of each element in Experiment 9a, but their performance measure as a ratio of the associative strengths of the elements at the correct corner over the associative strengths of all the elements at all the locations masks the superconditioning effect that is apparent when the associative strength of the geometric cue of the correct corner is compared across the two groups. One way to reconcile this problem is to revise Miller and Shettleworth's performance rule so it does not include a ratio. For example, one could assume that a simple subtraction rule governs the choice of which corner to visit in the rectangle, as shown in Equation 4.1 and expanded in Equation 4.2, where P is the performance measure, V_C and V_I are the total associative strengths of all the element in the correct and incorrect corners respectively, and G_C and G_I are the associative strength of the

geometric cues at the correct and incorrect corners, while B represents the associative strength of the common cue.

$$P = V_C - V_I \quad (\text{Equation 4.1})$$

$$P = (G_C + B) - (G_I + B) \quad (\text{Equation 4.2})$$

By using the equations above, the performance measure would be based solely on the associative strengths of the geometric cues present during test and result in a performance measure of 1.42 and 0.91 for the superconditioning and control groups respectively at the end of Stage 3. However, this rule would not be sufficient to explain the failure to find overshadowing. For instance, for the simulated overshadowing experiment in a triangle shown in Figure 1.4 (p. 38), applying the subtraction rule just described would result in the performance measure being 0.41 and 0.70 for the overshadowing and control groups respectively, a clear indication of overshadowing of geometric cues by a landmark. A worked example is provided below that implements the subtraction rule for the overshadowing experiment in the triangle just considered. P represents the performance measure, V_C , V_I and, V_A represents the total associative strength of all the elements presented in the correct corner, the incorrect corner, and the apex. G_C , G_I , and G_A represent the associative strength of the geometric cues at the correct and incorrect corners and the apex respectively. B is the associative strength of the common cue.

$$P = V_C - V_I - V_A \quad (\text{Worked Example})$$

$$P = (G_C + B) - (G_I + B) - (G_A + B)$$

Overshadowing Group

Control Group

$$P = (.38 + .23) - (-.13 + .23) - (-.13 + .23)$$

$$P = (.64 + .34) - (-.2 + .34) - (-.2 + .34)$$

$$P = .41$$

$$P = .70$$

The use of a subtraction rule to predict performance during tests on spatial tasks in environments with a distinctive shape then leads to the conclusion that perhaps a Rescorla-Wagner (1972) type rule is sufficient to explain superconditioning but not overshadowing and blocking in the spatial domain. More work is needed to develop a better performance measure that is capable of explaining the failures to find cue competition, as well as, the successful demonstrations of cue competition in the spatial domain. This does not, however, take away from the conclusions drawn from the present chapter. That is, the superconditioning effects found in the present chapter provides the most convincing evidence to date that learning in environments with a distinctive shape is governed by competitive learning rule.

We will now change focus slightly for the next two chapters to examine another limitation of Miller and Shettleworth (2007) introduced in Chapter 1 concerning their interpretation of potentiation of geometric cues by non-geometric cues.

Chapter 5: Between-cue associations influence searching for a hidden goal in an environment with a distinctive shape

5.1. Introduction

Previous chapters demonstrated that the associative model of learning about geometric cues proposed by Miller and Shettleworth (2007) does not provide a complete account of overshadowing, blocking and superconditioning in Chapters 2, 3, and 4 respectively. The limitations of the model are even more apparent when confronted with findings described by Graham et al. (2006) and Pearce et al. (2006).

As a reminder from Chapter 1, Pearce et al. (2006) trained rats to find a submerged platform in a right-angled corner of a kite-shaped arena. The walls creating the corner with the platform were white, and the remaining walls were black for an experimental group; whereas all four walls were white for a control group. A test trial in the absence of the platform was then conducted in a kite-shaped arena constructed from four white walls. Pearce et al. (2006) found that the experimental group spent more time during this trial searching in the correct corner than the control group. Even though the black walls were absent during the test trial, their presence during training appears to have potentiated learning about the position of the platform with reference to the shape of the arena. The manner in which the associative model of geometry learning explains the potentiation reported by Pearce et al. (2006) can be appreciated by focusing on the two right-angled corners of the kite. Graham et al. (2006) discovered that when rats are placed in a kite-shaped pool with a black and white corner they tend to head towards the corner created from the two black walls in preference to any other corner. Miller and Shettleworth (2007) therefore proposed that the salience of the black corner in the study by Pearce et al. (2006) was higher than of the white corner, and that the initial associative strength of the black corner was 0.3 whereas for the white corner it was zero. Given these assumptions, the Rescorla-Wagner (1972) equation

predicts that during the initial trials each approach to the incorrect corner will result in a greater decrement in the associative strength of the geometric cues created by the incorrect corner in the experimental than the control group. During the test in the white kite, the higher negative associative strength of the geometric cues for the incorrect corner in the experimental than the control group will then encourage the former group to spend more time than the latter in the correct corner.

There is, however, one reason for questioning whether the model of Miller and Shettleworth (2007) provides a satisfactory account for the potentiation that was reported by Pearce et al. (2006). This account depends crucially on the incorrect corner of the kite being created by black walls. If the converse arrangement is used, in which the correct corner is black and the incorrect corner is white then potentiation is not predicted to occur. Indeed, overshadowing is predicted in these circumstances. Contrary to this prediction, Experiment 1 by Graham et al. (2006) found a similar potentiation effect to that reported by Pearce et al. (2006) even though the walls creating the correct corner in the kite during training were both black and those creating the incorrect corner were white.

The demonstrations of potentiation by Graham et al. (2006) and Pearce et al. (2006) thus pose a problem for Miller and Shettleworth's (2007) model. The purpose of the remaining experiments is to seek a more satisfactory explanation for potentiation and then to explain its implications for Miller and Shettleworth. In seeking an explanation for these findings, it is worth noting that potentiation has been reported reliably using non-spatial tasks. Perhaps the explanation offered for these effects also applies to demonstrations of potentiation in spatial tasks.

An example of potentiation using a non-spatial task is provided by Rescorla and Durlach (1981) who gave one group of rats an odour, and another group an odour-flavour compound before they received an injection of lithium chloride. Subsequent tests with the

odour by itself revealed a stronger aversion in the group that was conditioned with the compound than with the odour by itself (see also Clarke, Westbrook & Irwin, 1979; Rusiniak, Hankins, Garcia, & Brett, 1979). Thus the presence of the taste facilitated the acquisition of the aversion to the odour. Rescorla and Durlach suggested that conditioning in both groups resulted in the growth of a weak association between the odour and illness. They further suggested that, for the group trained with the compound, two additional associations were formed: one between the flavour and illness and, the other, a within-compound association between the odour and the flavour. The presentation of the odour by itself would then excite in both groups a rather weak conditioned response by virtue of its direct association with illness. However, because of the within-compound association, the odour in the compound group would activate a representation of the flavour which would activate strongly the memory of illness and then encourage a stronger conditioned response than in the group trained with odour by itself. Support for this analysis can be found in an additional experiment described by Rescorla and Durlach in which subjects received conditioning with two odour-flavour compounds AX and BY. Flavour Y was then presented by itself for a revaluation phase in order to extinguish its association with illness. Subsequent test trials with the two odours revealed a stronger aversion to A than B. The explanation for this result is that when B was presented, even though it may have excited a representation of Y, the fact that this flavour could no longer excite a conditioned response meant that there was no additional support for the weak response that would result from the fragile association between the odour B and illness. In contrast, because both the direct and indirect associations of A with the US would be effective, this stimulus would be expected to elicit a strong CR when it was presented alone.

The explanation offered by Rescorla and Durlach (1981) for the potentiation of conditioning with an odour by a flavour points to a possible explanation for the findings

described by Graham et al. (2006) and Pearce et al. (2006). During the initial training in the kite, the experimental group might use the shape of the pool (or some component of the shape) and the colour of the walls as two distinct cues for finding the platform as in the Miller and Shettleworth (2007) model. However, they might learn to approach the geometric cues created by the correct corner, and to avoid those created by the incorrect corner; they might also learn to approach white and to avoid black. Associations might also develop between the geometric cues and the colour of the walls creating them. The sight of the incorrect geometric cues during the test in the white kite would then activate a memory of the aversive black walls and encourage the experimental group to swim away from this corner, and towards the correct corner. Likewise, the sight of the correct geometric cues might activate a memory of the attractive white walls and act as a further inducement for this group to approach the correct corner. In the control group, the correct and incorrect geometric cues would be associated with the same cue – white walls – and lead to the choice on the test trial being determined solely by the associative strengths of the two geometric cues. As a consequence, the preference for the correct over the incorrect corner in this group would be weaker than in the experimental group. The two reported experiments test the foregoing explanation for the results described by Graham et al. and Pearce et al., by using a similar methodology to that described by Rescorla and Durlach.

5.2. Experiment 10

During the first phase of the experiment, two groups of rats were required to find a submerged platform in one of the right-angled corners of a kite-shaped pool (see the left-hand side of Figure 5.1). The colour of the walls creating this corner was white, whereas the remaining two walls were black. After the completion of this training, the rats proceeded directly to a revaluation phase which took place in a square pool with one corner created from

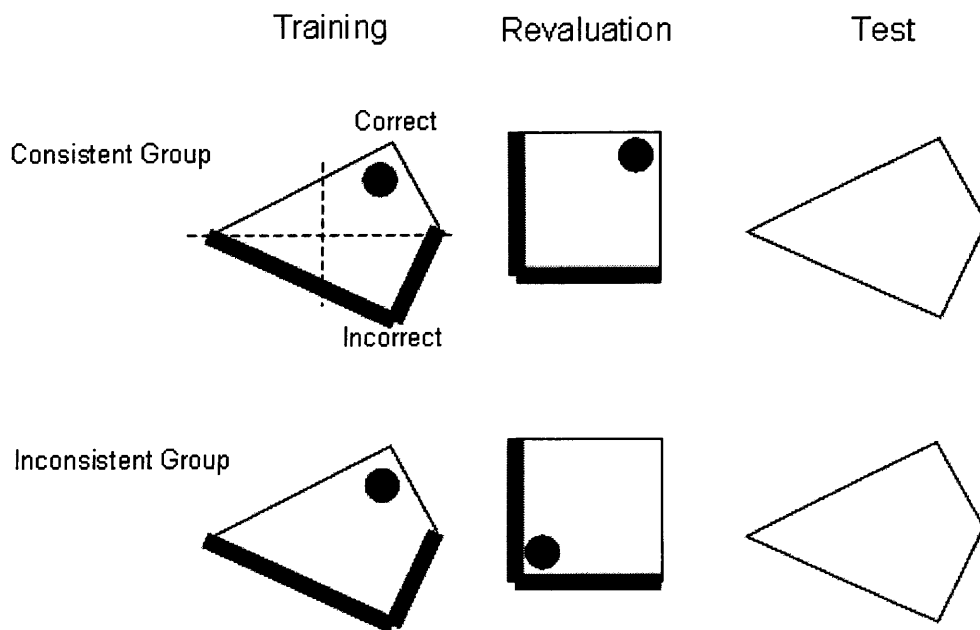


Figure 5.1. A plan of the apparatus used for the two groups in the three stages of Experiment 10. Thick lines indicate black walls, thin lines indicate white walls, dashed lines indicate how the arena was divided into quadrants for the purpose of analysing the results from the test trials. The black circle indicates where the platform was located.

two black walls and the opposite corner created from two white walls. The platform was located in the white corner for the consistent group, and in the black corner for the inconsistent group (see the centre column of Figure 5.1). As a result of their initial training, both groups would be expected to head initially for the white corner in the square, but gradually the inconsistent group should shift to a new strategy of heading directly for the black corner. This treatment was intended to result in the white walls being more attractive than black walls for the consistent group and the opposite being true for the inconsistent group. Finally, all rats received a single test trial in which they were placed in a kite-shaped pool constructed from four white walls and without a platform (see the right-hand side of Figure 5.1). If the initial training in the kite results in the formation of between-cue associations then, in the test trial, the sight of the incorrect corner will retrieve a memory of the black walls. Because the consistent group has just been trained to avoid black walls, and the inconsistent group to approach them, the influence of the between-cue associations would be to encourage the former group to swim away from the incorrect corner and the latter group to swim towards it. These differences should then result in the consistent group exhibiting a stronger preference for the correct over the incorrect corner than the inconsistent group.

Apart from anticipating that the preference for the correct over the incorrect corner will be stronger for the consistent than the inconsistent group, it is not possible to make a more precise prediction about the outcome of the test trial for the inconsistent group. During the training in the kite, this group will learn to approach the geometric cues created by the correct corner, and to avoid those created by the incorrect corner. During the training in the square it will learn to approach black and to avoid white. The geometric cues by themselves in the test trial will encourage the inconsistent group to head towards the correct corner and away from the incorrect corner. At the same time, these cues will activate representations of black and white, which will encourage rats to head towards the incorrect corner and away

from the correct corner. Depending on their relative strengths, the conflict between these tendencies could then result in the inconsistent group spending more time, less time, or the same amount of time in the correct than the incorrect corners of the test arena.

5.2.1. Method

Subjects and Apparatus. Sixteen naïve rats were of the same stock, approximately the same weight, and housed in the same manner as those in Experiment 1. The apparatus was the same as that used in Experiment 1 except a kite-shaped arena was used. To create the kite-shaped pool four Perspex boards were placed vertically in the pool and suspended by bars that extended over the edge of the pool. There were two long boards (1.8 m long, 0.59 m high, 2 mm thick) and two short boards (0.9 m long, 0.59 m high, 2mm thick). During the first stage of the experiment, both groups were trained in a kite-shaped pool in which one pair of adjacent long and short boards was black and the opposite pair was white. For the second stage, a square arena was used for the two groups. The walls of the arena were made from the same material as the walls for the kite but their length was 1.41 m. Two adjacent walls of the square were black and two adjacent walls were white.

Procedure. All sessions were conducted in the same manner as Experiment 1 except that four release points were used within a session (one for each wall of the kite). There were two stages of training in the present experiment. Stage 1 consisted of training in a kite-shaped arena and Stage 2 was a reevaluation phase which took place in a square arena. During Stage 1, the rats received 20 sessions of training. Rats were randomly assigned to the consistent and inconsistent group in equal numbers ($n=8$). The platform was located in the white, right-angled corner of the kite for all rats. For half the rats in each group this corner was created from a long wall to the left of a short wall whereas for the remaining rats the opposite right-

angled corner contained the platform. At the end of Stage 1, all rats proceeded directly to Stage 2.

For Stage 2 of training, the platform was located in the white corner of the square for the consistent group and the black corner for the inconsistent group. There were six sessions in Stage 2 with four trials in each session. Sessions 1 to 5 and the first three trials of Session 6 were conducted in the same manner as for Stage 1. The fourth trial in Session 6 was a test in which rats were released from the centre of the kite, which was constructed from four white boards, for 60 s with the platform removed from the pool.

As in previous experiments on training trials, a record was taken of whether, after being released, a rat entered first the correct corner of the pool – the corner containing the platform. The results from the test trial were analysed in the same manner as for the study by Graham et al. (2006). The kite-shaped pool was divided into two large and two small quadrants by drawing a line between the apex and the obtuse-angled corner and bisecting this line with a line that passed through it at 90°, as shown by the dashed lines in the upper left-hand panel of Figure 5.1. A record was taken of the amount of time spent in the correct quadrant (the one where the platform had been located in Stage 1) and the incorrect quadrant (the opposite quadrant). All other procedural details were the same as in Experiment 1

5.2.2. Results and Discussion

The left-hand panel of Figure 5.2 shows the mean percentages of correct choices for the two groups during the 20 sessions of training in the kite. Both groups started off by performing at chance and quickly improved so that for the majority of this stage they made a correct choice on virtually every trial. To compare the performance of the two groups, individual mean correct choices for the last three sessions combined were computed. An

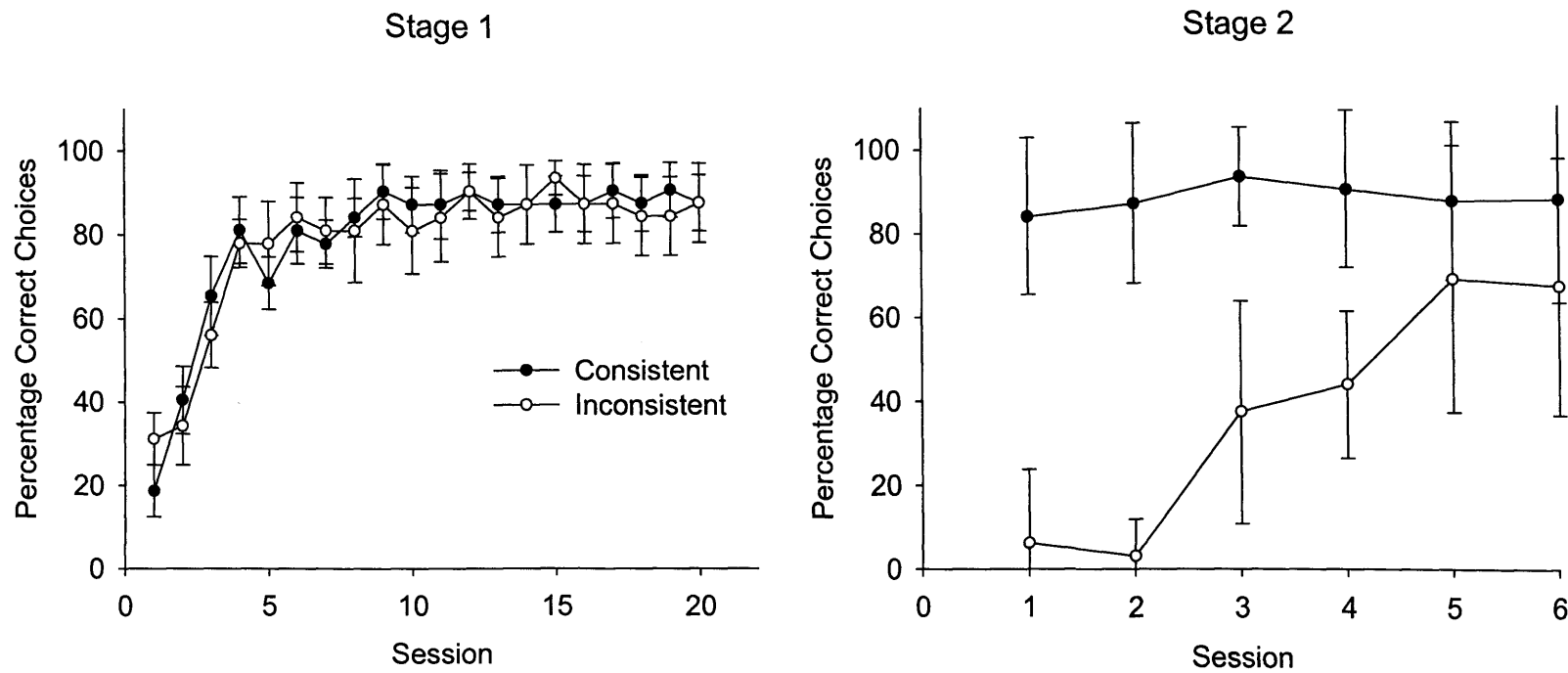


Figure 5.2. The mean (+SEM) percentages of correct choices made during each session of training in the kite (left-hand panel) and revaluation training in the square (right-hand panel) for the Consistent and Inconsistent groups of Experiment 10.

analysis of these scores failed to reveal a significant difference between the groups, Mann-Whitney $U(8, 8) = 28.5$.

The right-hand panel of Figure 5.2 shows the mean percentages of correct choices for the two groups during the training in the square. The consistent group swam to the correct corner on the majority of trials in every session, which should not be surprising because the colour of the corner containing the platform was the same as for the previous trials in the kite. The inconsistent group made virtually no correct choices when its training in the square commenced, but its performance improved gradually as training progressed. Once again, this pattern of results should not be surprising because the colour of the correct corner in the square was opposite to that for the kite. The final levels of performance of the two groups were compared by computing individual mean percentages of correct choices for the last three sessions in the square. Analysis of these mean percentages revealed a significant difference between the groups, $U(8, 8) = 8.5$. A further analysis on the last two sessions failed to reveal a significant difference between the groups, $U(8, 8) = 20.0$, thus by the end of the second stage of training, the consistent and inconsistent groups were performing equally.

The mean percentages of time spent in the correct and incorrect quadrants during the 60-s test trial are shown in Figure 5.3. It is clear that the revaluation treatment in the square was effective because the preference shown by the consistent group for the correct over the incorrect quadrant was not evident in the inconsistent group. The duration of time spent in the correct and incorrect quadrants for individual rats were analysed with a 2 X 2 ANOVA (group X quadrant) which revealed a significant effect of group, $F(1, 14) = 11.79$, of quadrant, $F(1, 14) = 6.35$, and a significant Group X Quadrant interaction, $F(1, 14) = 8.44$. Tests of simple main effects revealed that the consistent group spent a greater proportion of time in the correct quadrant than the incorrect quadrant, $F(1, 14) = 14.72$, while the

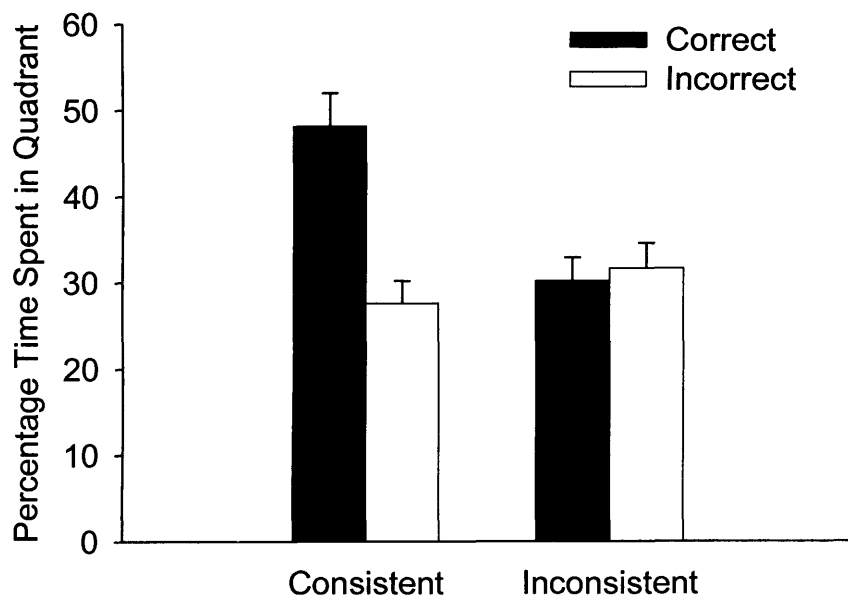


Figure 5.3. The mean (+SEM) percentages of time spent in the correct and incorrect quadrants during the test trial of Experiment 10.

inconsistent group had no preference for either quadrant $F < 1$. The consistent group spent more time in the correct quadrant than the inconsistent group, $F(1, 14) = 17.53$, and the time spent in the incorrect quadrant did not differ between the groups, $F < 1$.

The outcome of the test trial is entirely in keeping with predictions made in the introduction to the experiment. These predictions were based on the assumption that the initial training in the black and white kite would result in the formation of associations between, on the one hand, geometric cues created by the correct and incorrect corners and, on the other hand, the colour of the walls forming these corners. When subjects were returned to the kite for the test trial, the sight of the geometric cues would then remind them of the colours of the two corners during the training stage. The significance of the colours would, however, be determined by the training in the square which should encourage the consistent group to approach the correct corner and avoid the incorrect corner while the opposite tendencies would be expected for the inconsistent group.

A potential problem with the results from the inconsistent group is that during the test trial, a similar amount of time was spent in the correct and the incorrect quadrants. Moreover, since the correct and incorrect quadrants each occupied approximately one-third (34.6%) of the arena, the time spent in them during the test did not differ substantially from that expected if subjects searched for the platform at random. It is thus possible that the performance of the inconsistent group was not determined at all by the influence of between-cue associations or, for that matter, any other associations that were formed during the initial training in the kite. Instead, as a consequence of the training in the square, where the white corner was no longer associated with food, the inconsistent group might have acquired an aversion to approaching any corner that was white. The transfer of this response to the white kite for the test trial could then have encouraged the inconsistent group to avoid the four white corners and

resulted in a random search for the platform. The next experiment was conducted with this explanation in mind.

5.3. Experiment 11

Experiment 11 was based on the design of Experiment 10, with the following exceptions. First, in Stage 1, the colour of the correct and incorrect corners were counterbalanced, so that for half of the rats in each group the walls surrounding the correct corner were white and the walls surrounding the incorrect corner were black, with the opposite arrangement for the other half of each group. Second, at the end of the experiment there were two test trials in the kite with all four walls the same colour. The colour of the walls for the first test was the same as the incorrect corner during the initial training in the kite and, for the second test, the colour was the same as the correct corner during the initial training. The second test, therefore, was equivalent to the test trial in the previous experiment, and its outcome was expected to be similar to that reported above. A different outcome was, however, anticipated for the first test. On this occasion the inconsistent group was tested in an arena in which the colour of the walls was not associated with the absence of the platform, and thus the possible problem outlined above would no longer apply (although it might apply to the consistent group). Once again, it is not possible to derive precise predictions about the outcome of the first test for the inconsistent group, except that any influence of between-cue associations will result in the preference for the correct over the incorrect quadrant being larger in the consistent than the inconsistent group.

Finally, Experiment 11 differed from Experiment 10 by using a different measure of performance for the test trials. The correct and incorrect quadrants in the previous experiment each occupied approximately one third of the area of the kite and thus provided a rather insensitive measure of how much time subjects spent in the immediate vicinity of the

correct and incorrect corners. In order to provide a more accurate index of the preference for the region where the platform was located, for the present experiment the times that subjects spent in two circular search zones with a radius of 15 cm were reported. The centre of the correct search zone was coincident with the point where the centre of the platform was situated during the initial training in the kite. The centre of the second, incorrect zone was located in the equivalent position in the opposite corner. Each zone occupied 4.46% of the entire area of the kite. This method for recording the time spent in the correct and incorrect corners has already been used successfully in a kite by Pearce et al. (2006) as well as all the previous chapters of this thesis.

5.3.1. Method

Subjects and Apparatus. The 32 rats were from the same stock and housed in the same manner as for Experiment 10. At the start of the experiment the rats were assigned at random and in equal numbers to the two groups. The apparatus was the same as for Experiment 10, with the addition of a short and a long black wall that were used to construct a kite with four black walls for the test trials.

Procedure. For the 20 sessions of Stage 1, the two groups were required to find a submerged platform in one of the right-angled corners of a kite-shaped pool. One of the corners in the pool was constructed from two white walls and the other corner was constructed from two black walls. The platform was located in the black corner for half the rats in each group and in the white corner for the remaining rats. Within each of these subgroups the platform was located in a corner where the long wall was to the left of the short wall for four rats and in the opposite corner for the remaining four rats. The method of training was the same as for Experiment 10.

For the seven sessions of Stage 2 the two groups were required to find a submerged platform in one corner of a square pool. One of the corners in the pool was made from two white walls, and the opposite corner was made from two black walls. The platform was located in the corner of the same colour as the corner where the platform had been located in Stage 1 for the consistent group. For the inconsistent group the colour of the corner containing the platform was opposite to the colour of the correct corner in Stage 1. The fourth trials of Sessions 6 and 7 of this stage were tests conducted in a kite with four walls of the same colour and with the platform removed from the pool. The colour of the walls during the first test were the same as the colour of the walls surrounding the incorrect corner in Stage 1 for all rats, whereas for the second test they were the colour of the walls surrounding the correct corner. The remaining procedural details were the same as for Experiment 10.

5.3.2. Results and Discussion

The mean percentages of trials on which the two groups made a correct choice during each session of training in the kite are presented in the left-hand panel of Figure 5.4. In keeping with the results from Experiment 10, both groups soon headed directly for the correct corner on being released into the pool. A Mann-Whitney test, based on individual mean percentages of trials on which the correct corner was approached for the last three sessions combined confirmed that there was no difference between the performance of the two groups, $U(16, 16) = 110.5$. The consistent group headed directly towards the corner containing the platform on nearly every trial throughout the training in the square, as shown in the right-hand panel of Figure 5.4. The inconsistent group started this stage by being reluctant to head toward the corner with the platform, but eventually this corner was approached directly on the majority of trials. A comparison of individual mean percentages of trials on which the corner with the platform was approached first for the final three sessions combined revealed a

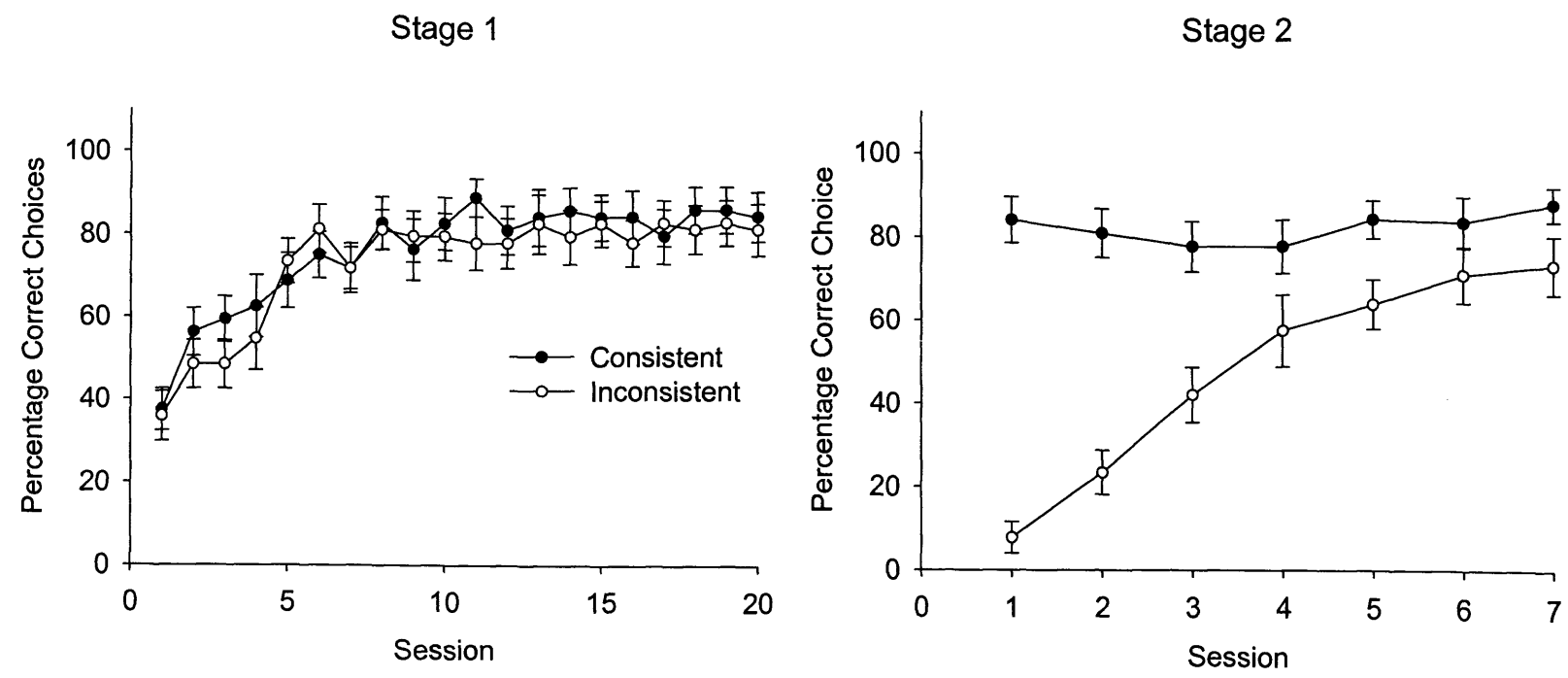


Figure 5.4. The mean (+SEM) percentages of correct choices made during each session of training in the kite (left-hand panel) and revaluation training in the square (right-hand panel) for the Consistent and Inconsistent groups of Experiment 11.

difference between the groups, $U(16, 16) = 66.5$. A follow up analysis on the last two sessions combined revealed no significant difference, $U(16, 16) = 79.5$, thus by the end of Stage-2 training, the two groups were performing equally.

The results from the first test trial, which took place in a pool with four walls of the same colour as the incorrect corner for the training in the kite, can be seen in the left-hand panel of Figure 5.5. In contrast to the results from the previous experiment, the inconsistent group exhibited a substantial preference for the incorrect over the correct zone, whereas the consistent group expressed only a slight preference for the correct over the incorrect zone. A two-way ANOVA revealed a significant effect of group, $F(1, 30) = 11.44$, and a significant Group x Zone interaction, $F(1, 30) = 6.89$, but the effect of zone was not significant, $F(1, 30) = 1.73$. Tests of simple main effects revealed that the inconsistent group spent significantly more time in the incorrect than the correct zone, $F(1, 30) = 7.77$, but the equivalent comparison for the consistent group was not significant, $F < 1$. Furthermore, the inconsistent group spent significantly more time in the incorrect zone than the consistent group, $F(1, 60) = 18.06$, but the time spent by the groups in the correct zone was not significantly different, $F < 1$.

In order to determine if significantly more time was spent in a search zone than would be expected if rats searched at random in the pool during the test trial, a series of one-sample t tests was conducted. The tests compared the percentage of time spent by a group in a search zone with 4.46. This value is the percentage of the pool that was occupied by a 30 cm diameter search zone and represents the percentage of time subjects would be expected to remain in a search zone if they swam randomly throughout the pool. The amount of time spent in the incorrect, $t(15) = 7.77$, and the correct, $t(15) = 2.64$ search zones was significantly greater than that expected on the basis of chance for the inconsistent group, but not for the consistent group, $t_s(15) < 1.46$.

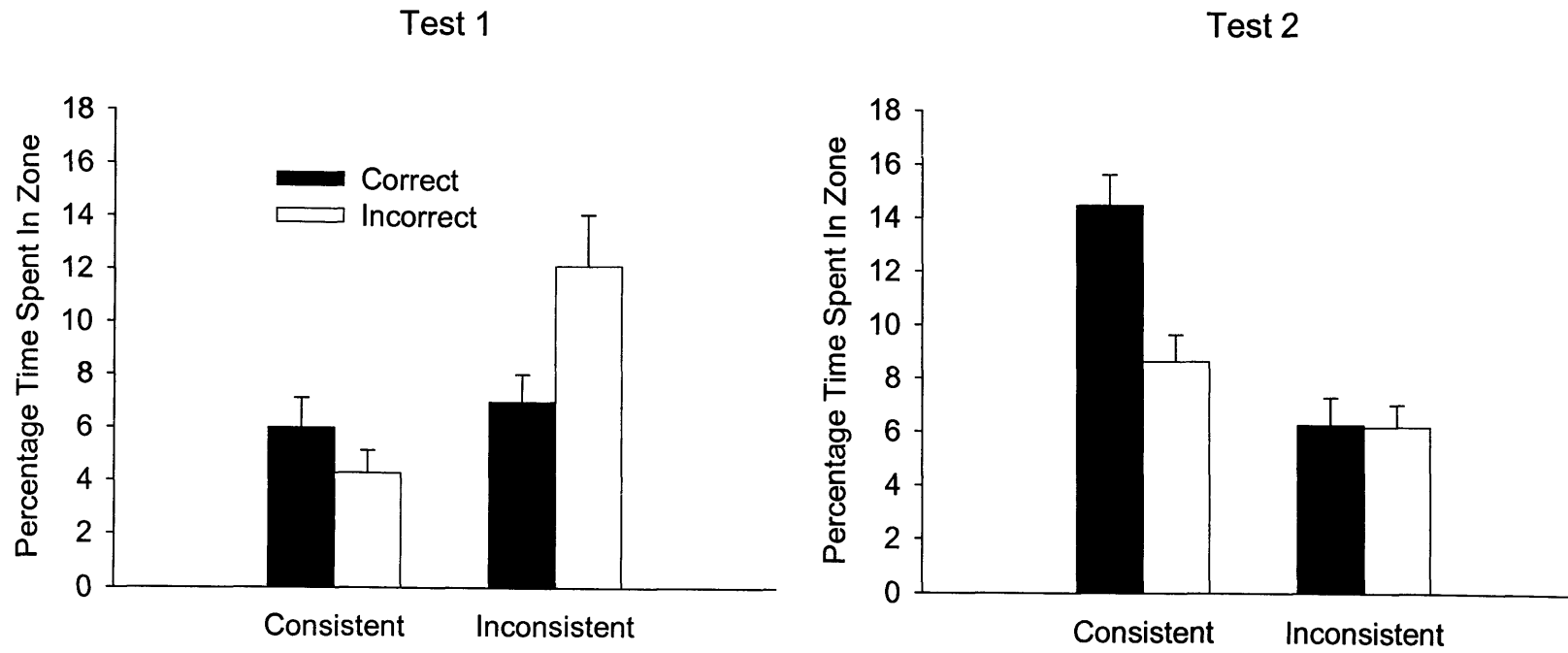


Figure 5.5. The mean (+SEM) percentages of time spent in the correct and incorrect zones during Test 1 (left-hand panel) and Test 2 (right-hand panel) of Experiment 11.

The results from the second test trial (see the right-hand panel of Figure 5.5) resembled closely those from Experiment 10. The consistent group spent substantially more time in the correct than the incorrect zone, whereas the inconsistent group spent approximately the same amount of time in both zones. A similar ANOVA to the one just described revealed a significant effects of group, $F(1, 30) = 41.84$, and zone, $F(1, 60) = 6.51$, and a significant interaction, $F(1, 30) = 6.17$. Tests of simple main effects confirmed that the consistent group spent significantly more time in the correct than the incorrect zone, $F(1, 30) = 12.67$, and significantly more time in the correct zone than the inconsistent group, $F(1, 30) = 33.42$. The inconsistent group did not spend significantly more time in one search zone than the other, $F < 1$, and did not differ from the consistent group in the amount of time spent in the incorrect zone, $F(1, 30) = 3.02$.

A set of one-sample t tests, similar to those described for the first test trial revealed that the consistent group spent significantly more time than would be expected on the basis of chance in both the correct $t(15) = 8.99$ and the incorrect, $t(15) = 4.21$, search zones. In addition, despite appearances to the contrary in Figure 5.5, the time spent by the inconsistent group in the incorrect zone was significantly greater than chance, $t(15) = 2.17$, but the equivalent comparison for the time spent in the correct zone was not significant, $t(15) = 1.83$.

The most important finding from the experiment is the greater preference for the incorrect than the correct zone by the inconsistent group during the first test trial. This finding demonstrates that the revaluation treatment in the square during the second stage of the experiment reversed the preference for the correct over the incorrect corner initially acquired by the inconsistent group in the kite. A ready explanation for this outcome is that during the initial training, associations formed between the geometric cues of the two corners and their respective colours. The sight of the correct corner during the first test trial would then activate the memory of the colour that it was originally, and since this colour during the

second stage was associated with the absence of the platform, subjects would seek to minimise their contact with this corner in the test trial. Conversely, the sight of the incorrect corner would activate the memory of a colour that had been rendered attractive during the revaluation stage and subjects would be expected to approach this corner. It is worth noting that the influence of the between-cue associations was substantial, because the experience with the geometric cues during the original training in the kite should have resulted in the inconsistent group approaching the correct and withdrawing from the incorrect corner during the test trial. The finding to the contrary indicates that the influence of the between-cue associations was so profound in the inconsistent group that not only did it nullify the direct influence of the geometric cues, but it additionally resulted in a reversal of the preference controlled by them.

The poor performance of the consistent group in the first test matches closely the poor performance of the inconsistent group in the second test. Both sets of results were from tests conducted in a kite whose walls were the same colour as the corner that subjects had to avoid during their training in the square. It thus appears that when subjects are placed in an arena where every corner is the same colour as one they have just avoided they may swim at random, avoiding all corners, and it becomes difficult for any associations based on geometric cues, either direct or indirect, to influence performance.

The pattern of results from the second test trial are sufficiently similar to the outcome of the first experiment, that it would seem reasonable to conclude that the change in the measure of performance has not affected at all the outcome of the experiment. In support of this conclusion the results from both test trials were reanalysed using the same measure of performance as that adopted in Experiment 10. The overall pattern of results was similar to that shown in Figure 5.5. For the first test, the mean percentage of time spent in the correct and incorrect quadrants were 36.0 and 28.4 respectively for the consistent group, and 27.4

and 39.6 for the inconsistent group. For test 2, the mean percentage of time spent in the correct and incorrect quadrants were 38.6 and 28.4 respectively for the consistent group and 32.4 and 33.0 for the inconsistent group.

5.4. Summary and Conclusions

Rats were trained in two experiments to find a platform in a kite-shaped pool. The platform was located in a right-angled corner whose walls were of a different colour to the walls creating the opposite right-angled corner. When rats were subsequently tested in a pool with four walls of the same colour, the preference for the correct over the incorrect corner was stronger if they had been trained to approach rather than to avoid the colour of the originally correct corner during an intermediate phase of the experiment. The results imply that the initial training permitted the development of associations between the geometric cues defining each corner and its colour. On being placed in the arena for the test trial, the sight of the geometric cues would then activate a representation of their colour during the initial training, and the tendency to approach the corner would be influenced by whether or not the colour was still attractive. These findings, and the interpretation offered for them, are similar to experiments that have investigated taste-aversion conditioning with a compound comprising a taste and an odour (e.g. Rescorla & Durlach, 1981). These results are also similar to findings recently described by Rhodes, Creighton, Killcross, Good, and Honey (2009) from an experiment conducted in a rectangular arena with food buried in one corner. The between-cue associations in Rhodes et al., as here, were between geometry and local cues. It thus appears that between-cue associations can influence performance in a wide variety of settings.

There are two conclusions that can be made on the basis of the experiments presented in this chapter. First, Miller and Shettleworth's (2007) model provides an incomplete

account of potentiation. Second, between-cue association form during spatial tasks. The next chapter will explore implications of the second conclusion and Miller and Shettleworth's account of overshadowing.

Chapter 6: Between-cue associations form between a landmark and geometric cues in an environment with a distinctive shape

6.1. Introduction

The experiments thus far provide mixed support for the proposals of Miller and Shettleworth (2007). The results described in Chapter 4 provide compelling evidence that spatial learning about combinations of geometric and non-geometric cues is governed by an error-correction rule similar to that proposed by Rescorla and Wagner (1972), and which has been incorporated into the model put forward by Miller and Shettleworth. However, this model predicts that overshadowing should occur in certain circumstances, and my experiments failed to confirm these predictions. Moreover, if my modification to the choice rule is accepted, then the majority of failures of overshadowing will pose a problem to this rule. Certain results from my blocking experiments also posed a problem for the model of Miller and Shettleworth.

The previous chapter has shown that during a spatial task associations can develop between geometric and non-geometric cues. The purpose of the present chapter is to explore whether it is possible and justifiable, to appeal to these cues in order to explain the findings that appear to pose a problem to Miller and Shettleworth's model. Theoretically, at least, it is possible to explain the failures to detect overshadowing in Chapter 2 by referring to these associations. For clarification, take for example a simple overshadowing experiment in a triangular swimming pool. An overshadowing group was trained to find a submerged platform in one of the corners of the triangle near a landmark. A control group was trained in a similar fashion except no landmark was presented. During a test trial in the triangle with the landmark and platform removed, the overshadowing and control groups spent approximately the same time searching in the vicinity of where the platform was located, This outcome suggests that in the overshadowing group, the landmark failed to restrict

learning about geometric cues. An explanation based on between-cue associations suggests that for the overshadowing group, the animals may form three associations. First a direct association with the landmark and the location of the platform may be formed, along with a direct association between the geometric cues of the environment and the location of the platform. The third association that may form is a between-cue association between the landmark and the geometric cues of the environment. The control group, in this example, would only form a direct association between the geometric cues of the environment and the location of the platform. During test in the absence of any landmarks, the control group has to rely on the strength of the association between the geometric cues and the location of the platform. The overshadowing group also has the direct association between the geometric cues and the location of the platform, but this would be relatively weak because the landmark would be expected to overshadow learning about geometric cues. In addition to that association, the presence of the geometric cues during the test trial would also activate a representation of the landmark via the between-cue association formed during training, which would indirectly activate the relatively strong association between the landmark and the location of the platform. This additional benefit of having a between-cue association between the landmark and the geometric cues may then compensate for an overshadowing effect, and thus results in no overshadowing. This explanation can also account for other failures of overshadowing.

The majority of the studies that report a failure to see overshadowing and blocking use either distinct landmarks (Hayward et al., 2003, 2004; Pearce et al., 2001) or small panels attached to the walls forming the shape (Kelly et al., 1998; Wall et al., 2004). The foregoing explanation for the failure to find cue competition in terms of between-cue associations assumes that the results reported in Chapter 5 can generalise to instances where the landmark is a distinct object such as a sphere or small black panels attached to the walls of the

environment rather than the non-geometric cue being the colour of the walls forming the shape. An obvious next step is to examine if the results reported in Chapter 5 can be attained when the cue is a discrete landmark rather than the colour of the walls. The following experiments explored this idea.

6.2. Experiment 12

Rats completed two stages of training. During Stage 1, they were required find a submerged platform located in one of the corners at the base of a triangular-shaped pool. An overshadowing group received one landmark located in the same corner as the platform and a different landmark in the symmetrically opposite corner without a platform. The landmarks were either a sphere that hung directly above the platform, or two black panels attached to the walls creating the corner. The type of landmark was counterbalanced throughout the entire experiment. The control group was trained in the same way as the overshadowing group except that the landmarks in the corners at the base of the triangle were identical. When given a test trial in the absence of the platform and any landmarks, it was found that the landmarks in the overshadowing group had not restricted learning about the location of the platform with respect to geometric cues. Following this test trial, the overshadowing group received an additional 8 sessions of training to ensure between-cues associations had enough time to form between the landmark and the geometric cues at the correct corner. This group then proceeded onto Stage 2 to determine if these associations may have compensated for an overshadowing effect.

During Stage 2, rats in the overshadowing group were randomly divided into consistent and inconsistent groups and underwent landmark revaluation training in a square-shaped pool. The consistent group was trained with the platform in one corner of the square near to the landmark that was reinforced in Stage 1. The landmark that was non-reinforced in

Stage 1 was located in the diametrically opposite corner and was still non-reinforced. The inconsistent group received identical training except that the landmark that was reinforced in Stage 1 was now non-reinforced in the square, and the landmark that was non-reinforced in Stage 1 was reinforced in the square.

If between-cue associations form during the initial training between the geometric cues of the triangular arena and the landmarks at each location, the consistent group should show a preference for the correct corner over the incorrect corner during a test trial in the triangle following revaluation training in the square. Presumably, following revaluation training, when a rat is placed in the triangle, the geometric cue of the correct corner will activate a representation of the landmark at that corner and since that landmark was reinforced in Stage 2 rats should be more willing approach the correct rather than the incorrect corner. For the inconsistent group, the geometric cues similarly will activate a representation of the landmark at each respective corner, but unlike the consistent group, the landmark at the correct corner in the triangle was non-reinforced during Stage 2 and thus rats should be reluctant to enter this corner. On the basis of these considerations the inconsistent group should show a weaker preference for the correct corner in the triangle than the consistent group following revaluation training. Depending on the strength of the associations formed between the landmark and the location of the platform during Stage 2, the inconsistent group could show a preference for the correct corner over the incorrect corner (albeit a much smaller one than in the consistent group), or they could show no preference for either corner, or they could even show a preference for the incorrect corner over the correct corner.

6.2.1. Method

Subjects and Apparatus. The 32 rats were from the same stock, of approximately the same weight, and housed in the same manner as in Experiment 1. All the rats were previously used in an appetitive conditioning experiment, but had no experience in a swimming pool. The apparatus was identical to that used in Experiment 1 except for the following exceptions. Two different types of landmarks were used in this study. First, a black spherical landmark, 11 cm in diameter was used. The second landmark consisted of two black panels (21 cm X 29.7 cm) that could be attached (via surface tension) to the walls forming a corner in such a way that the edges of each panel made contact in the corner of the triangle.

During Stage 1, rats were trained in a triangular-shaped pool constructed from the same material as in Experiment 1. In Stage 2, rats were trained in a square shaped pool constructed from four, white boards (1.41 m long, 0.59 m high, and 2 mm thick)) made from the same materials as the triangle.

Procedure. The experiment consisted of two training stages. Stages 1 and 2 were conducted in a triangular and square-shaped pool respectively. Rats were randomly assigned to two groups in equal number ($n = 16$): an overshadowing group and a control group. During the 22 Sessions of Stage-1 training, the overshadowing group received the platform 25 cm from one of the corners at the base of the triangle on an imaginary line that bisected the corner. For half of the rats, a spherical landmark was located 33 cm, directly above the platform and two black panels were attached to the symmetrically opposite corner. The remaining rats received the converse arrangement with the black panels attached to the corner where the platform was located and the sphere in the opposite corner. Half of the rats received the platform in one corner at the base of the triangle and the other half received the platform in the opposite corner at the base of the triangle. The control group received identical training except all rats received two identical landmarks, one in the each corner at

the base of the triangle. For half of the rats these landmarks were spheres and for the other half the landmarks were black panels.

The first three trials of Sessions 14 were conducted in the same manner as described previously. The fourth trial of this session was a geometry test. During the test trial, the platform and landmarks were removed from the pool. The rats were released from the centre of the arena and allowed to swim for 60 s. Following testing, the overshadowing group continued training in the triangle for an additional seven sessions before proceeding to Stage 2.

Stage 2 was a revaluation stage conducted in a square-shaped arena, which consisted of 6 Sessions. Rats from the overshadowing group were randomly divided into two groups of equal number ($n = 8$): a consistent group and an inconsistent group. The consistent group received the platform located in one of the corners of the square near the landmark that indicated the platform location in Stage 1. The landmark that signalled the absence of the platform in the Stage 1 was located in the diametrically opposite corner in the square and still signalled the absence of the platform. For instance, rats that received the spherical landmark above the platform in Stage 1 and the black panels in the opposite corner, now received the spherical landmark above the platform and the panels in the diametrically opposite corner in Stage 2. The inconsistent group received the platform in one of the corners of the square near the landmark that signalled the absence of the platform in Stage 1, while the other landmark that signalled the platform in Stage 1 was located in the diametrically opposite corner in the square. The first three trials of Session 6 were conducted in the same manner as previous training trials in the square. The fourth trial was a geometry test conducted in the triangular arena in the absence of the platform and landmarks.

All other procedural details were identical to Experiment 1.

6.2.2. Results and Discussion

Figure 6.1 shows the percentage of correct choices across the 22 sessions of training during Stage 1. Note that training with the control group ceased after Session 14. The overshadowing group performed markedly better than the control group making correct choices on virtually every trial at the end of training, while the control group was relatively poorer. A Mann Whitney U test conducted on the individual mean percentage of correct choices combined across the last three sessions before the first geometry test (i.e., Sessions 12, 13, and 14) revealed that this difference was significant, $U(16, 16) = 1.0$.

The left-hand panel of Figure 6.2 shows the results of the first geometry test for the full 60-s test trial. Both groups spent more time in the correct zone than the incorrect zone but the time spent in the correct and incorrect zones was similar for the overshadowing and control groups. A 2 X 2 (Group X Zone) ANOVA was conducted and revealed a significant zone effect, $F(1, 30) = 36.43$. The group effect and the Group X Zone interaction were not significant, $F_s < 1$.

To some extent, there is a precedent in the literature to analyze the first 15 s of test trial. Pearce et al. (2001) suggest this to be a more sensitive measure of performance on test trials. Thus to ensure that an overshadowing effect is not being masked by the later part of the test trial, the first 15 s were analyzed. The right-hand panel of Figure 6.2 shows time spent in the correct and incorrect search zones for the first 15 s of the test trial. The results are very similar to those of the full 60-s test trial. A 2 X 2 (Group X Zone) ANOVA was conducted and revealed a significant zone effect, $F(1, 30) = 20.78$. The group effect and the Group X Zone interaction were not significant, $F_s < 1$.

Figure 6.3 shows the percentage of correct choices across Stage 2 training. A rat was deemed to have made a correct choice in the square if it had entered the corner that contained

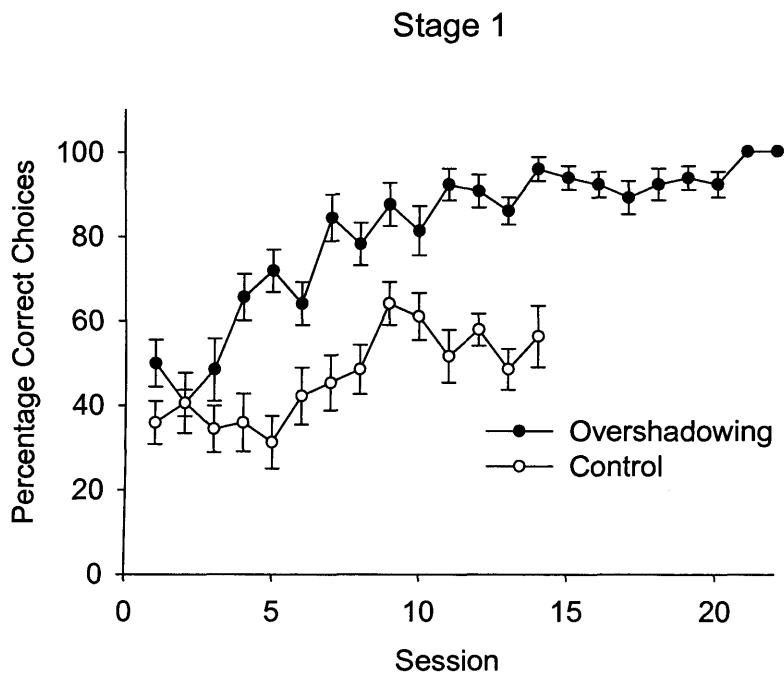


Figure 6.1. Mean (+SEM) percentage of correct choices during Stage 1 for the overshadowing and control groups of Experiment 12.

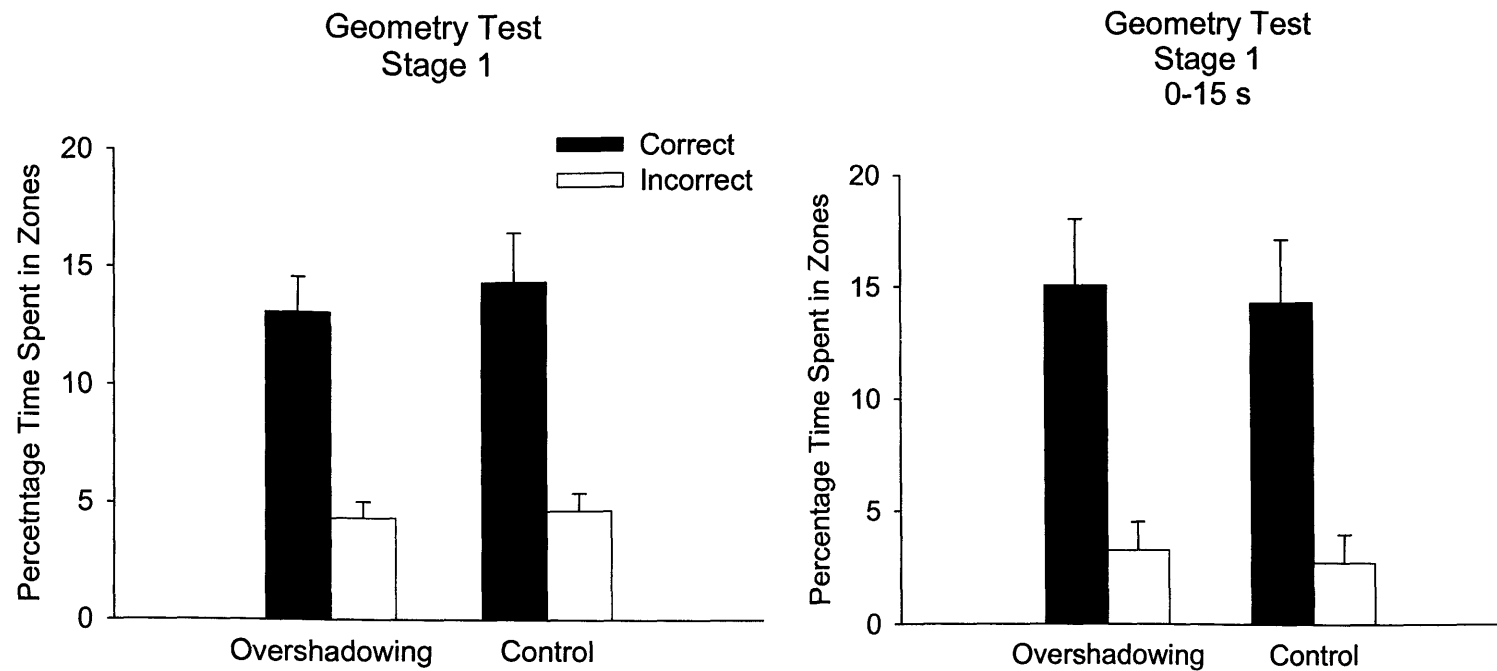


Figure 6.2. Left-hand panel: The mean (+SEM) percentage of time spent in the correct and incorrect zones during a 60-s geometry test in Session 14 for the overshadowing and control groups of Experiment 12. Right-hand panel: The mean (+SEM) percentage of time spent in the correct and incorrect zones during the first 15 s of the same geometry test of Experiment 12.

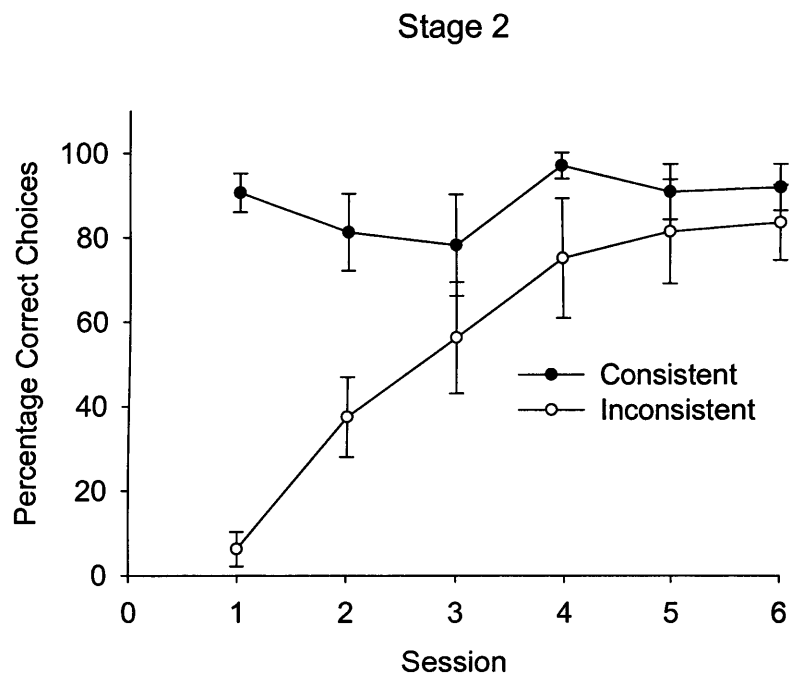


Figure 6.3. Mean (+SEM) percentage of correct choices across Stage 2 for the consistent and inconsistent groups of Experiment 12.

the platform on its first choice. If the rat first entered any of the remaining three corners, an incorrect choice was recorded. It is apparent that the consistent group readily made correct choices after the transition to Stage 2. This outcome was expected because the landmark that was a reliable predictor of the platform during Stage 2 was the same as the one that was close to the platform in Stage 1. In contrast, the performance of the inconsistent group was rather poor at the outset of Stage 2. Again this result was expected because the landmark that was a reliable predictor of the platform during Stage 1 was now non-reinforced in Stage 2.

Although rats in the inconsistent group showed poorer performance at the beginning of training, they quickly began making correct choices on the majority of trials. A Mann Whitney U test conducted on the individual mean percentage of correct choices combined across the last three sessions revealed no difference between the groups, $U(8, 8) = 23.0$.

Figure 6.4 shows the results from the geometry test after completion of Stage 2 training, for the full 60 s (left-hand panel) and for the first 15 s (right-hand panel) of the test trial. For the full 60-s test trial, the consistent group spent more time in the correct zone than the inconsistent group, however a 2 X 2 (Group X Zone) ANOVA revealed no significant group effect, $F(1, 14) = 2.56$, no zone effect, $F(1, 14) = 3.35$ and unfortunately no Group X Zone interaction, $F < 1$. As can be seen in the right-hand panel of Figure 6.4, when the first 15 s of the test trial was analyzed, the consistent group spent a greater proportion of time in the correct zone, and the inconsistent group spent a greater proportion of time in the incorrect zone. A similar analysis to the one conducted for the full 60-s test trial revealed no group or zone effects, $F_s < 1$, but the Group X Zone interaction was significant, $F(1, 14) = 4.63$, $p = 0.05$. None of the simple main effects were significant.

It is clear from the results from Stage 1 that a landmark does not restrict learning about the location of the platform with respect to geometric cues. This was true when an

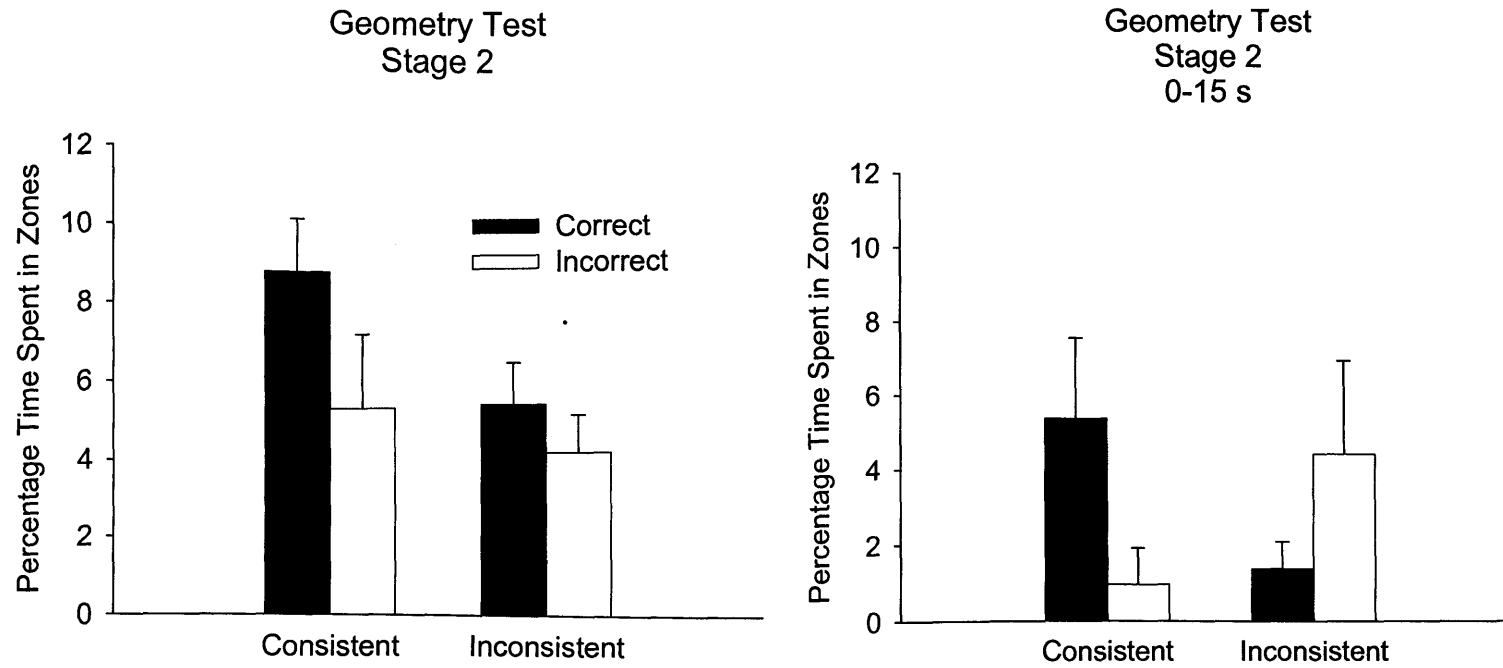


Figure 6.4. Left-hand panel: The mean (+SEM) percentage of time spent in the correct and incorrect zones during a 60-s geometry test in the triangle following Stage 2 for the consistent and inconsistent groups of Experiment 12. Right-hand panel: The mean (+SEM) percentage of time spent in the correct and incorrect zones during the first 15 s of the same geometry test conducted.

analysis on the full 60-s test trial was conducted as well as an analysis on the first 15 s of the test trial where the differences between the groups, if present, were expected to be more pronounced. There are multiple reasons why a landmark and geometric cues might appear not to compete with each other. First, there may in fact be no competition between landmarks and geometric cues. Each cue type may be encoded by independent systems that do not interact with each other (Cheng, 1986; Gallistel, 1990). Second, it is possible that between-cue associations formed between the landmark and geometric cues in the overshadowing group. The additional association between the landmark and geometric cues in the overshadowing group may then compensate for any overshadowing effect. These additional associations would not benefit rats' performance in the control group because identical landmarks were located in both the correct and incorrect corners of the triangle. Stage 2 attempted to look at this possibility.

After reevaluation training, it is clear that when the first 15 s of the test trial was analyzed, not only did the consistent group spend a larger proportion of time in the correct corner than the incorrect corner, the inconsistent group showed a complete reverse pattern of behaviour, spending more time in the incorrect corner than the correct corner. Presumably, when rats were placed in the triangle, the geometric cues of the correct and incorrect corners activated representations of the landmarks at those locations. Since during Stage 2, rats in the inconsistent group were reinforced to go to the landmark that was in the incorrect corner in Stage 1, rats would then be more willing to approach the incorrect corner during the final test trial than the consistent group.

These results support the proposal that between-cue associations form between landmarks and geometric cues. Experiment 13 was conducted in order to confirm the reliability of this effect.

6.3. Experiment 13

The finding of the previous experiment was relatively weak, only reaching significance when the first 15 s of the test trial was analyzed. It is reasonable to assume that these effects of between-cue associations are relatively small, therefore, in order to detect any differences, statistical power would need to be quite high. The present experiment attempts to increase power of detecting a difference and thus reinforce the conclusions drawn from the results of Experiment 12. There are two ways in which power can be easily increased, both of which were adopted for the present study. First, the number of subjects in each of the consistent and inconsistent groups was increased from 8 to 16 and, secondly, a within-subjects design was adopted to overcome the problem of high between-group variance.

There were two stages of training in this experiment. Stage 1 consisted of training in two different environments, a triangle and a rectangle. The two landmarks that were used were identical to those used in Experiment 12. For ease of exposition, the terms LM-T and LM-R will be used to refer to the two landmarks which were counterbalanced with respect to the training condition. In the triangle, the platform was located in one of the corners at the base of the triangle near LM-T. In the rectangle, the platform was located in one of the corners near LM-R. Stage 2 was a revaluation stage in a square pool. Half the rats received reinforced trials with LM-T and non-reinforced trials with LM-R, while the remaining rats received reinforced trials with LM-R and non-reinforced trials with LM-T. During reinforced trials the platform was located in a corner near the landmark. On non-reinforced trials the landmark was in one of the corners but with the platform removed from the pool. Thus rats were allowed to swim around the pool for 60 s before being removed. After Stage 2 training, rats were tested in both the triangle and rectangle in the absence of the platform and landmarks. See Table 6.1 for a summary of the design.

Table 6.1. *Design of Experiment 13 showing training environments and the landmarks that were present during each stage of the experiment. LM-T and LM-R refers to the landmarks that were reinforced in the triangle and rectangle during Stage 1 respectively.*

Group	Stage 1		Stage 2 - Revaluation in Square	
	Triangle	Rectangle	Reinforced Trials	Non-Reinforced Trials
Triangle Consistent	LM-T	LM-R	LM-T	LM-R
Rectangle Consistent	LM-T	LM-R	LM-R	LM-T

The rationale for the predicted outcome of the experiment is the same as in Experiment 12. For rats that received reinforced trials with LM-T and non-reinforced trials with LM-R, they should show a preference for the correct corner over the incorrect corner when tested in the triangle and show less of a preference for the correct corner in the rectangle. For the remaining rats that received reinforced trials with LM-R and non-reinforced trials with LM-T, rats should show a preference for the correct corner over the incorrect corner in the rectangle and less of a preference for the correct corner in the triangle.

6.3.1. Method

Subjects and Apparatus. The 32 rats were from the same stock, of approximately the same weight, and housed in the same manner as in Experiment 12. As in the previous experiment, all rats were previously used in an appetitive conditioning experiment, and had no experience in a swimming pool. Three shapes were used in this experiment. A triangular and square environment identical to that used in Experiment 12 and a rectangular environment constructed from 2 long (1.8 m long, 0.59 m high, and 2 mm thick) and 2 short (0.9 m long, 0.59 m high, and 2 mm thick) boards made from the same material as the other arenas. All other details concerning the apparatus were the same as in the previous experiment. The two landmarks were the same sphere, and the same black panels that were used in Experiment 12. Their position with respect to the platform was the same as for Experiment 12.

Procedure. There were two stages in this experiment. In Stage 1, rats received 14 sessions of training in the triangle and 14 sessions of training in the rectangle. In each environment, the platform was always located in the same corner. For half the rats the platform was always beneath the sphere in the triangle, and in the corner containing the two black panels in the rectangle. Only a single landmark and platform was present in the arena at

any given time. The opposite assignment of landmarks to the two environments was used for the remaining rats. For the sake of convenience the landmark in the triangle is referred to as LM-T, and in the rectangle as LM-R.

Stage 2 was a revaluation stage conducted in a square arena and consisted of eight sessions with two reinforced trials (i.e., the platform was present and located near a landmark) and two non-reinforced trials (i.e., the platform was absent but a landmark was situated in one of the corners). For non-reinforced trials, a rat was released from the centre of the pool and allowed to swim for 60 s before being removed and returned to its holding container. At the start of this stage, the rats were assigned at random to the two groups. Half of the rats – the triangle consistent group – received reinforced trials with LM-T and non-reinforced trials with LM-R while the other half of the rats – the rectangle consistent group – received reinforced trials with LM-R and non-reinforced trials with LM-T. The first two trials of Sessions 6 and 8 were conducted in the square in the same manner as the other trials with one reinforced trial and one non-reinforced trial. The third trial of Session 6 was a test trial in which half of the rats in each group were tested in the triangle and the other half tested in the rectangle. The third trial of Session 8 was also a test trial conducted in the opposite arena to that used in the previous test trial. During test trials, the platform and the landmarks were removed from the pool. The results from the test in the triangle were analyzed in the same manner as the previous experiment. The results from the test in the rectangle were analyzed in a similar manner except that the time spent in the correct zone was calculated by summing the time spent in the correct zone where the platform had been located during Stage 1 and the zone in the diagonally opposite corner. The time spent in the remaining two, incorrect, zones, were also combined. Any procedural details omitted were identical to previous experiments that were trained in an arena with a triangle (Experiment 1) and a rectangle (Experiment 9a).

6.3.2. Results and Discussion

Figure 6.5 shows the mean number of correct choices across Stage-1 training. For both environments, rats started making approximately 50% correct choices and towards the end of training were making correct choices on the majority of trials. A binomial test was conducted for the results from each environment to see whether each group was performing better than chance (33.3% in the triangle, and 50% in the rectangle) at the end of training. The percentage of correct choices was combined across the last three sessions. The number of rats performing greater than chance in the triangle was 32/32, and the number of rats performing greater than chance in the rectangle was 31/32. The binomial test revealed that in both environments rats were performing significantly better than chance.

The left-hand panel of Figure 6.6 shows the percentage of correct choices in the square during Stage 2 for the reinforced and non-reinforced trials separately for the triangle consistent and the rectangle consistent groups. There is rather little evidence on this measure of rats solving the discrimination. In the triangle consistent group, performance on the two trial types were similar in the number of correct choices made across training to the reinforced and the non-reinforced landmark. A Mann Whitney U test was conducted on the individual mean percentage of correct choices combined across the last three trial blocks and revealed no difference between the groups, $U(16, 16) = 120.5$. However, in the rectangle consistent group, on the non-reinforced trials rats made fewer correct choices as training progressed than on reinforced trials, indicative of them learning which landmark predicted a reinforced trial or non-reinforced trial. An analysis conducted in the same manner as in the triangle revealed a difference between the two trial types, $U(16, 16) = 24.0$.

Another measure of performance during non-reinforced trials was also taken. The right-hand panel of Figure 6.6 shows the proportion of time spent searching in a zone near the landmark during non-reinforced trials. As before, a search zone had a diameter of 30 cm with

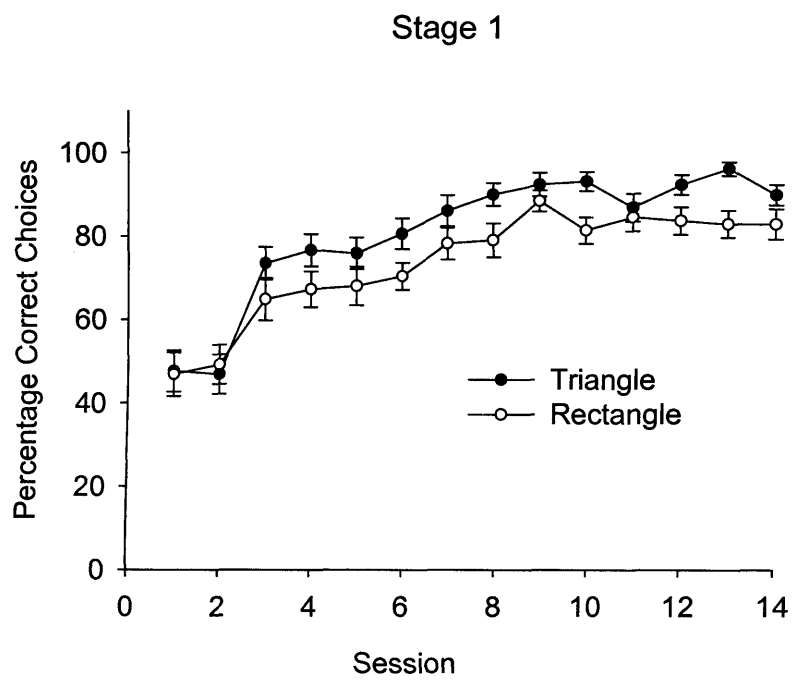


Figure 6.5. The mean (+SEM) percentage of correct choices across Stage-1 training in the triangle and rectangular environments of Experiment 13.

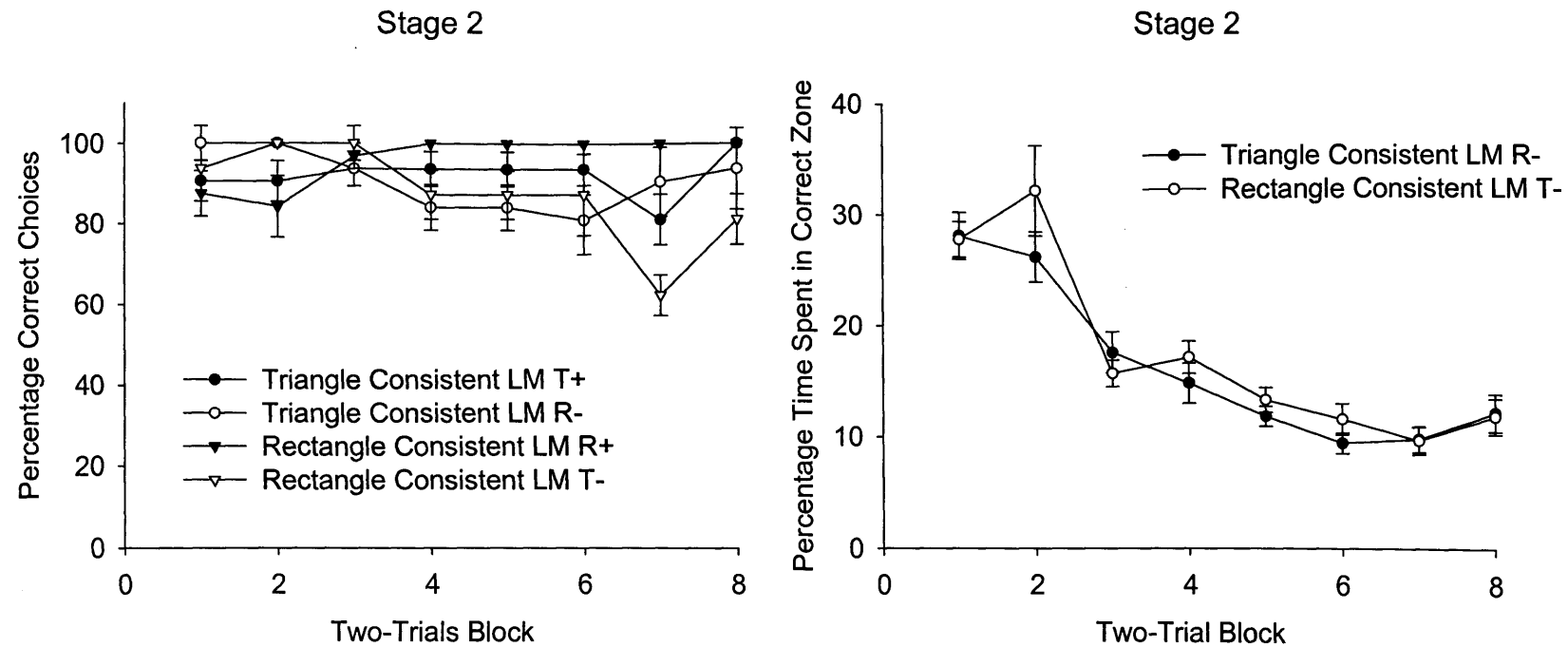


Figure 6.6. Left-hand panel: The mean (+SEM) percentage of correct choices across Stage 2 for the triangle consistent and rectangle consistent groups of Experiment 13. LM T and LM R refer to the landmarks that were reinforced in Stage 1 in the triangle and rectangle environments respectively. + and - refer to whether during Stage 2 the landmark was reinforced or non-reinforced respectively. Right-hand panel: The mean (+SEM) percentage of time spent in correct zone during non-reinforced trials during Stage 2 in the triangle consistent and rectangle consistent groups of Experiment 13.

its centre positions 25 cm for a corner on a line that bisected the corner. In both environments, both groups decreased their time spent in the vicinity of the non-reinforced landmark in the square as training progressed. The purpose of this stage was to extinguish conditioned responding to the landmark and thus it appeared to be successful. A paired *t*-test was conducted on the mean percentage of time spent in the correct zone on the first and last trial block for each group and revealed significant differences, $t_s(15) > 6.80$.

The left-hand panel of Figure 6.7 shows the time spent in the correct and incorrect corner for the test trial in the triangle. The triangle consistent group showed a preference for the correct zone over the incorrect zone, while the rectangle consistent group showed no such preference. A 2 X 2 (Group X Zone) ANOVA revealed a significant zone effect, $F(1, 30) = 4.5$, and a significant Group X Zone interaction, $F(1, 30) = 5.71$. The group effect was non-significant, $F < 1$. A simple main effects analysis was conducted on the interaction and revealed that the consistent groups spent a significantly greater proportion of time in the correct over the incorrect zone, $F(1, 30) = 10.18$. The consistent group also spent significantly more time in the correct zone than the inconsistent group, $F(1, 60) = 5.11$. The time spent in the incorrect zone between the two groups and the time spent in the correct and incorrect zone for the inconsistent group was not significant, $F_s < 2.41$.

The right-hand panel of Figure 6.7 shows the time spent in the correct and incorrect zones for the test trial in the rectangle. The rectangle consistent group showed no preference for either zone, and the triangle consistent group showed a preference for the incorrect over the correct zone. A 2 X 2 (Group X Zone) ANOVA revealed no significant main effects of group, zone and no significant Group X Zone interaction, $F_s < 3.19$.

The results from the test trial in the triangle indicate the influence of between-cue associations between the landmark and the geometric cues on spatial learning in environments with a distinctive shape. The preference for the correct over the incorrect

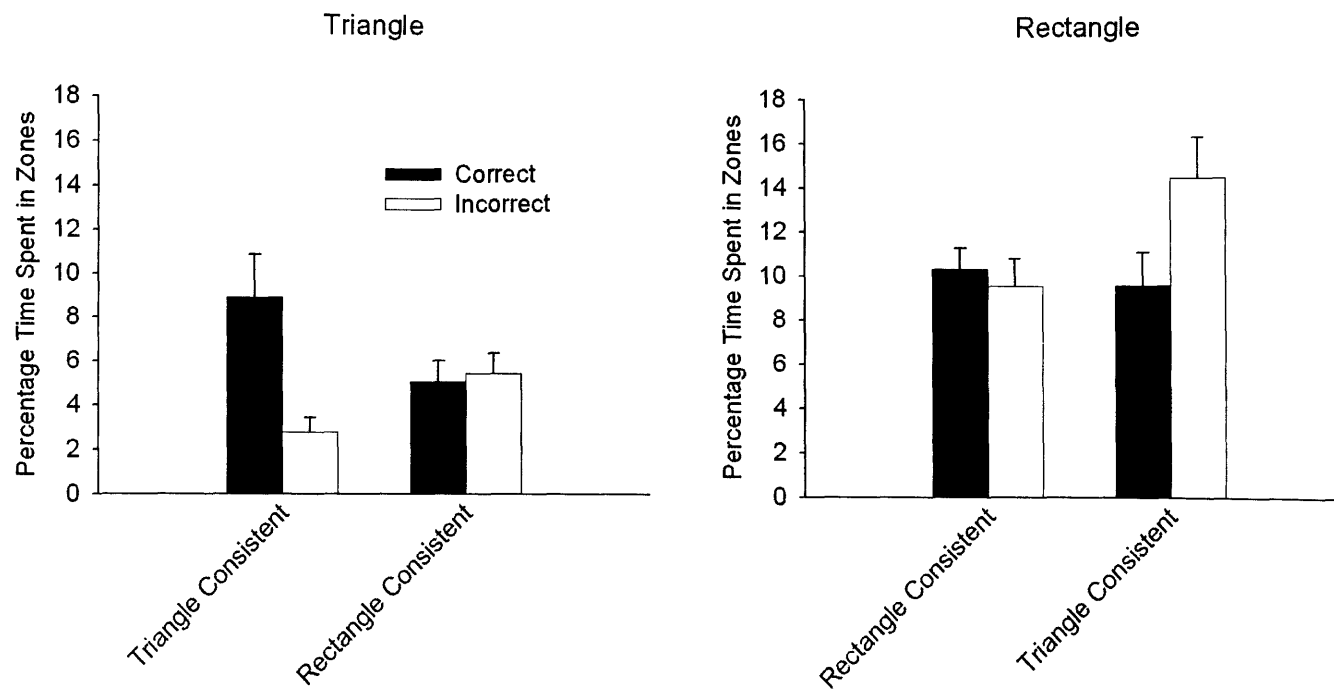


Figure 6.7. The mean (+SEM) percentage of time spent in the correct and incorrect zones during a geometry test in the triangle (left-hand panel) and rectangle (right-hand panel) following Stage-2 training for the triangle consistent and rectangle consistent groups of Experiment 13.

corner in the triangle consistent group is likely to have occurred because the sight of the geometric cues at the correct corner activated a representation of the landmark at that location. Since the triangle consistent group received reinforced trials with that same landmark during Stage 2, rats would be more willing to approach the correct corner in the triangle. In contrast, the rectangle consistent group received non-reinforced trials with the landmark (essentially extinction trials) in Stage 2. This training would lead rats to be less willing to enter the correct corner than the incorrect corner. This is clearly what happened in the triangle because the inconsistent group showed no preference for either the correct or the incorrect corner.

In the rectangle, there appears to be only slight evidence of the influence of between-cue associations. Rats showed no preference for either corner in the rectangle consistent group and showed a somewhat surprising preference for the incorrect corner in the triangle consistent group. There is no adequate explanation for this effect. One could possibly explain the preference for the incorrect corner in the triangle consistent group by appealing to between-cue associations, since the revaluation of the landmark during Stage 2 may stop rats from entering the correct corner in the rectangle, and drive rats to the incorrect corner, but the absence of a preference observed in the rectangle consistent group poses a problem because it is hard to understand why between-cue associations would influence behaviour in the triangle consistent groups and not the rectangle consistent group. It appears that in the triangle, between-cue association between a landmark and geometric cues influences behaviour, and in the rectangle, they do not. I shall consider a possible explanation for this outcome in the following section.

6.4. Summary and Conclusions

The experiments reported in this chapter extend the conclusions drawn from Chapter 5. Not only can between-cue associations influence spatial learning in environments with a distinctive shape when the walls forming the shape are different colours, but as Experiments 12 and 13 have shown, between-cue associations can also form between the geometric cues of the environments and individual landmarks. This was particularly true in a triangular shaped environment (Experiments 12 and 13). In contrast, no convincing evidence of between-cue associations was observed in the rectangular pool (Experiment 13).

There are two possibilities of why associations between the geometric cues and the landmark may not have been effective in the rectangle. First, during training prior to reevaluation, rats received a single platform in a corner of the rectangle with the landmark near it. However, in the rectangle, there are two corners that have identical geometric properties. One is the corner containing the platform, and the other is the diagonally opposite corner. Thus it follows if the rats make incorrect choices to the corner diagonally opposite to the corner containing the platform, they experience the geometric cue of the correct corner in the absence of the landmark which would decrease the strength of the between-cue association between the landmark and geometric cue of the correct corner. Essentially, the association that is formed between the geometric cue of the correct corner and the landmark is partially reinforced and as such may not be as strong as if the geometric cue of the correct corner is always paired with the presence of the landmark as in the triangle. During testing in the rectangle following reevaluation of the landmark, the strength of the between-cue association may be relatively weak and thus not influence, to a noticeable extent, learning about geometric cues in the rectangle.

Another explanation for the failure to find evidence of between-cue associations is that between-cue associations do not form as readily in rectangular environments as they do in other shaped environments such as the kite and triangle. Why this would be the case is not

entirely clear, but it seems to be in line with the results of Pearce et al. (2006) that showed that coloured walls potentiated learning about geometric cues in the kite, but overshadowed and blocked learning in the rectangle. This is of course assuming that the formation of between-cue associations results in the potentiation effect observed. If this explanation is correct, it then follows that because in the rectangle, between-cue associations do not form or are relatively weak and exert little influence on learning about geometric cues, then overshadowing and blocking can be observed because these effects are not masked by a between-cue association between the geometric cues and the landmark.

If the assumption that between-cue associations mask any blocking or overshadowing effects in learning in environments with a distinctive shape, how do the present results fit with the findings from Chapter 3 that demonstrated successful blocking of geometric cues by a landmark when the landmark was given extended pre-training? One can easily accommodate the results from Chapter 3 within the framework of between-cue associations by appealing to attentional processes. First, in the group of rats that received extended pre-training with the landmark during the first stage, they may focus all of their attention on the landmark. In the second stage where geometric cues were introduced, the rats may continue to focus their attention on the landmark and thus pay less attention to geometric cues. This explanation can not only explain the blocking effect, but given this explanation, there would be very little opportunity for the rats to form a between-cue association between the landmark and geometric cues and thus there is no possibility that the between-cue association could mask the blocking effect. But attention paid to the geometric cues would be substantially higher in rats that only received limited Stage-1 training. If this is the case, then an association may be able to form more readily between the geometric cues and the landmark and thus compensate for any blocking effects.

The reported experiments in Chapters 5 and 6 indicate that between-cue associations develop during spatial learning. These associations could be of considerable theoretical importance because they may explain the failure to observe cue competition effects in certain spatial tasks. It remains for future research to determine whether between-cue associations are effective in this way. Given the ambiguities with the results in the rectangle, it may therefore be sensible to regard between-cue associations as a possible rather than a certain explanation for the failure of landmarks near a goal to restrict learning about geometric cues provided by the shape of the environment.

Chapter 7: General Discussion

An important aim of this thesis has been to evaluate the proposal by Miller and Shettleworth (2007) that learning about the geometric cues in an environment with a distinctive shape is governed by the Rescorla-Wagner (1972) rule. One of the strengths of the proposals of Miller and Shettleworth has been its ability to explain a number of reported failures of a landmark to overshadow (Hayward et al., 2004; Hayward et al., 2003; Pearce et al., 2001) or block ((Hayward et al., 2004; Hayward et al., 2003; Wall et al., 2004) learning about the position of a goal relative to the shape of the environment. The success of their model in this respect is largely due to the choice rule proposed by Miller and Shettleworth. According to this rule the probability of choosing a corner on any trial is given by the ratio of the total associative strength of the corner in question over the total associative strength of all the locations in the environment (see Equation 1.3, p. 35). Using this choice rule typically masks any cue competition effects that are apparent in the acquired associative strengths of each cue. For instance, in an overshadowing or blocking study, by the end of the experiments the model predicts that the associative strength of the geometric cue of the correct corner in an experimental group is considerably smaller than in a control group, but the choice rule masks this difference for reasons explained on pages 36-39. This choice rule thus allows the model to successfully predict the failure to find overshadowing and blocking. However, my experiments have failed to lend these proposals of Miller and Shettleworth much support.

I demonstrated in Chapter 2 that the choice rule will no longer mask the effects of overshadowing if the salience of the geometric cue is relatively low. The experiments designed to test this prediction failed to confirm it. In Chapter 3, I demonstrated the model predicts blocking of geometric cues by a landmark will be observed, if extended training with the landmark is given. Although I successfully demonstrated blocking of geometric cues in those circumstances, the results from Chapter 3 were not in total compliance with the model

of Miller and Shettleworth. Instead, they were better explained by assuming the landmark and geometric cues were in a competition for attention rather than associative strength. Chapter 4 provided the most convincing evidence that learning about geometric cues is governed by the principles of associative learning by successfully demonstrating superconditioning with these cues. However, Miller and Shettleworth's model again failed to predict this outcome.

The observation of superconditioning in Chapter 4 is worth noting because the model predicts the associative strengths of the geometric cues of the correct corner for the superconditioning and control groups will be higher for the former than the latter group by the end of training. Clearly superconditioning with the geometric cues is predicted to take place. The problem, as I demonstrated in Chapter 4, is that the choice rule prevents this superconditioning from manifesting itself.

The results of the experiments reported in Chapters 2, 3 and 4 suggests the need to consider if the choice rule of Miller and Shettleworth (2007) can be revised in order for their model to accurately describe successful demonstrations of cue competition when geometric cues are involved in spatial tasks. Interestingly, their model does very well when predicting the acquisition of associative strength of all the cues during training in most environments. It is only when implementing the choice rule on a particular test trial, where one or more cues may be absent from the environment, that the choice rule becomes problematic. One obvious way to revise their model is to implement a different choice rule. The choice rule that was suggested in the conclusions for Chapter 4 is to take the difference between the associative strength of the correct corner and the associative strengths of the incorrect corners. Rather than using a ratio measure as proposed by Miller and Shettleworth, this new performance rule assumes that the behaviour of an animal on a trial is governed by the difference between the associative strength of the correct and incorrect corners rather than a ratio of these strength.

Although this revised performance rule successfully predicts superconditioning, it fails to predict instances in which no overshadowing or blocking has been found. In those circumstances, the revised performance rule predicts overshadowing and blocking (see the worked example, p. 138). This is very much consistent with a direct application of the Rescorla-Wagner (1972) model.

The benefit of the suggested performance rule is that it is not technically a choice rule, *per se*. The revised performance rule does not allow one to calculate the probability of choosing the correct corner on a given trial, as with Miller and Shettleworth's (2007) model. Greater values on the performance measure would indicate a greater influence over behaviour than smaller values. For instance, for the superconditioning example (see top of p. 138), the difference in associative strengths of the correct and incorrect corners was 1.42 and 0.91 for the superconditioning and control groups respectively. These values indicate that for the superconditioning group, the correct corner will have a greater influence over behaviour than in the control groups. However, if one takes the performance rule as correct, then why was overshadowing and blocking of geometric cues not observed in the past studies? A trivial explanation for this result is that overshadowing and blocking paradigms are not sensitive enough to enable cue competition to be observed. Perhaps overshadowing and blocking would be found with extended training. We know from Chapter 3 that extended pre-training with the landmark resulted in blocking, but extended training in an overshadowing experiment in Chapter 2 did not result in overshadowing (see Figure 2.4, p. 55). In this experiment, a geometry test trial was given on Session 12 and then again on Session 24 and in both cases, no overshadowing was observed. Perhaps even further training would have resulted in overshadowing, but how many sessions would be necessary is not entirely clear.

Given that the revised performance rule is able to predict superconditioning, this outcome makes it a more favourable rule over Miller and Shettleworth's (2007) choice rule to

explain learning in environments with a distinctive shape. However, there are still some reservations with the revised performance rule as it cannot reconcile the failures to find overshadowing and blocking of geometric cues in past studies. The failure to find a suitable choice rule to explain the interaction between landmarks and geometric cues indicates the need to seek an additional explanation for my results. One possibility can be based on between-cue associations.

7.1. Implications of Between-Cue Associations

In Chapters 5 and 6, it was successfully demonstrated that rats formed between-cue associations between geometric and non-geometric cues. The existence of these associations provide the basis for an alternative account of potentiation and may also help explain the failure to find overshadowing and blocking in the spatial domain. Theoretically, it is possible that overshadowing and blocking are present in the reported cases where no effects of cue competition were found, but these effects were masked by between-cue associations that formed between the geometric and the non-geometric cues during training. For example, in Chapter 2, a two-landmark control group was trained specifically because the model of Miller and Shettleworth predicts overshadowing when such a control is used. In contrast to their predictions, no overshadowing was observed. In both the overshadowing and the two-landmark control groups, associations may have formed between the geometric cues of the correct location and the platform. However, in the overshadowing group additional associations could form between the landmark and the platform and between the landmark and the geometric cues. The presence of these additional associations in the overshadowing group would then benefit the rats during test trials when only geometric cues were present because the sight of the geometric cues at the correct location would activate the association between the geometric cues and the platform as well as the associations between the

geometric cues and the landmark. The summation of these associative links in the overshadowing group could then compensate for any overshadowing effect resulting from the presence of the landmark during training. For the two-landmark control group, between-cue associations could have formed between the landmark and the geometric cues at the correct location, but the presence of the landmark at the incorrect position would also promote a between-cue association to form between the landmark and the geometric cues at the incorrect location. During test trials in the absence of the landmark, the sight of the correct or the incorrect corner would activate a representation of the landmark and promote choices of similar strength to both the correct and incorrect locations resulting in no increased benefit in searching in the correct zone of the pool.

If between-cue associations mask any overshadowing effects, then the same could be said for blocking. This, however, is contrary to the results of Chapter 3, where successful blocking was demonstrated. Blocking was found only in the blocking-24 group which received 24 sessions of pre-training with the landmark but not in the blocking-12 group that only received 12 sessions of pre-training with landmark. It is possible that the blocking-12 group formed a between-cue association between the landmark and the geometric cues of the environment during Stage 2 and these associations masked the blocking effect. For the blocking-24 group, a between-cue association may not have formed or may not have exerted much of an influence on spatial behaviour. This difference between the groups can be explained by appealing to attentional processes similar to the explanation provided in the conclusions to Chapter 3. The blocking-12 group may not have fully attended to the landmark at the outset of Stage 2 and thus paid attention to the geometric cues. This would allow between-cue associations to form between the landmark and the geometric cues, and effectively mask any blocking. In contrast, the blocking-24 group may have focused all of its attention on the landmark at the outset of Stage 2 and thus paid very little attention to the

geometric cues. One would not expect a between-cue association to form between the landmark and the geometric cues in this instance and thus the influence of between-cue associations would be minimal. Similarly, in Chapter 4, superconditioning is unlikely to be influenced by between-cue associations because during the second stage of the experiments rats were given an A+/AX- discrimination. Any between-cue association that may have formed between A and X on AX- trials would be diminished during trials in which A was reinforced alone.

Theoretically, if one acknowledges the presence of between-cue associations, then all the results reported in the present thesis, as well as the past failures to find cue competition between geometric and non-geometric cues, can be explained. However, to do this, one must rely on a number of assumptions about the relative strength of these associations under different conditions. Nevertheless, spatial theories such as Miller and Shettleworth may benefit from acknowledging the presence of between-cue associations. Before making any further conclusions on the importance of between-cues associations, a related topic of potentiation needs to be addressed.

7.2. Implications of Findings for Potentiation in the Spatial Domain

Potentiation of learning about geometric cues has only been observed in two studies (Graham et al., 2006; Pearce et al., 2006). In both cases, different coloured walls forming the correct and incorrect corners of a kite-shaped pool potentiated learning about the geometric cues of the environment. The results described in Chapter 5 suggest a possible explanation for these results based on between-cue associations. The experiments demonstrated that an association formed between the coloured walls and geometric cues of a kite-shaped environment. These associations would then provide an additional source of support for finding the platform during testing in a kite-shaped pool with walls a uniform colour. The

sight of the correct corner would activate directly an association between the geometric cues of that corner and the location the platform. In addition, the geometric cues of the correct corner could indirectly activate the association between the coloured walls of the pool and the location of the platform via a between-cue association between the geometric cue of the correct corner and the colour of the walls. This additional benefit would not be present in a control group that did not receive training with the coloured walls or in a control group where the coloured walls were made unreliable for finding the platform.

Several questions arise from this explanation of potentiation. First, why does one not see potentiation in a rectangular environment when rats are trained in a similar experimental design to that described above? For example, Pearce et al. (2006) trained rats to find a platform in one corner of a rectangular pool where the corner containing the platform was constructed from white walls and the diagonally opposite corner was constructed from black walls. In this instance, the coloured walls overshadowed, not potentiated, learning about the geometric cues. Why this is the case is not entirely clear. One possible explanation is that the geometric cues in the rectangle are greater in salience than the coloured walls, while in the kite, the geometric cues are less salient than the coloured walls. We know from taste aversion studies in Pavlovian conditioning that a strong cue potentiates a weak cue, but a weak cue does not potentiate a strong cue (Bouton, Dunlap, & Swartzentruber, 1987). If the same principles can be applied to spatial learning, then it follows that potentiation of learning about geometric cues would only occur if the salience of the non-geometric cues were greater than the geometric cues. Thus the relative salience of the geometric cues in the kite and rectangle must differ, with the geometric cues in the kite being less salient than in the rectangle. There is some evidence for this conclusion. During the first stage of Experiments 9a and 9b, rats were trained to locate a goal in a corner of the rectangle and kite respectively (Figure 4.6, p. 121). As can be seen, the asymptote that is reached by the end of 20 sessions

of training is approximately 92% and 75% correct choices in the rectangle and kite respectively. Learning about geometric cues in the kite proceeded more slowly than in the rectangle, indicative of the salience of the geometric cues in the kite being less than in the rectangle.

Another point that needs to be considered before concluding this section is why a landmark, such as a beacon attached to the goal, does not potentiate learning about geometric cues in the same way as coloured walls do? For example, in one experiment by Graham et al. (2006; Experiment 2), a group was trained to find the hidden platform in one corner of a kite-shaped pool, with a landmark attached to the platform. In this instance, the landmark neither potentiated nor overshadowed learning about geometric cues compared to a group that received the same training except in the absence of the landmark. One possibility for this outcome is that landmarks do not form between-cue associations with geometric cues as readily as coloured walls and thus potentiation does not occur. However, this is unlikely given the results of Chapter 6 showing that landmarks do indeed form between-cue associations with geometric cues in some environments. In fact there is some evidence that landmarks potentiate learning about geometric cues from Experiment 3 in Chapter 2. An overshadowing group was trained to find a platform underneath a hanging landmark in a triangular pool. A control group received the same training except an additional, identical, landmark was located in the opposite corner. During testing in the absence of the platform and any landmarks, rats in the overshadowing group spent a greater proportion of time in the correct zone than the control group during the first test trial in Session 12 and the second test session on Session 18 (see Figure 2.9, p. 67). However, this difference was not significant, and was not reliable, as the difference was not apparent during the test trial on Session 24. It remains for future research to determine the factors that promote such facilitation effects on learning about geometric cues.

Before concluding this section, it is important to consider how likely it is that between-cue associations contribute to the failures to find cue competition and to the successful demonstrations of potentiation. Given the result from Chapter 6, between-cue associations did not form as readily in the rectangle, but even in the triangle the strength of the between-cue associations were relatively weak. It is hard to argue forcefully that such limited and small effects could have a large influence on whether one sees potentiation and cue competition. Given the mixed result in the literature of when cue competition occurs it is worth noting the possibility that learning about geometric cues may not follow associative learning principles under certain circumstances. With this in mind, it may be worth returning to the idea that spatial learning is not always governed by an error correction rule. I have already argued that there is good reason for rejecting the proposals of Cheng's (1986) and Gallistel's (1990) geometric module, but a number of less extreme versions of their proposal have been advocated, and it is worth exploring whether they can explain my results.

7.3. Implications of Findings for Cheng and Newcombe's (2005) Modular Theories

Cheng's (1986) and Gallistel's (1990) initial proposal of learning about geometric cues suggested that geometric cues were encoded in a geometric module that is resistant to non-geometric information. However, as was noted in Chapter 1, this idea of an impermeable geometric module has not gained universal acceptance. In particular, the results by Graham et al. (2006) and Pearce et al. (2006) that showed potentiation of learning about geometric cues by non-geometric cues posed a major problem for this idea. Given these findings, Cheng (2008) retracted his view of a purely geometric module void of any influence by non-geometric information. The results from the present thesis are also in line with this change of mind. The successful demonstration of blocking of geometric cues by a landmark further suggests that learning about geometric cues is not resistant to non-geometric cues. Also, the

results of Chapter 4, suggest that non-geometric cues can influence learning about geometric cues, by showing superconditioning of geometric cues by an inhibitory landmark. There are, however, two additional revised geometric modular accounts that need to be discussed.

Cheng and Newcombe (2005) considered two ways in which the claim about a geometric module might be relaxed in order for learning about geometric and non-geometric cues to interact. One possibility is that non-geometric features can be pasted onto a geometric representation in a modular subsystem (Cheng, 1986), but it is noted that “pasting of features is sometimes not done” (p. 17). It is also the case that this “pasting” was not assumed to influence what was learned about the geometric cues. Clearly, the evidence of blocking and superconditioning in Chapters 3 and 4 go against this claim. Another possibility that Cheng and Newcombe suggested was that inputs to the learning process were modular, but then geometric and non-geometric information are combined before they influence behaviour. The implication for the present thesis for this last point of view is that a theory such as that advocated by Rescorla and Wagner (1972) provides a good account of how learning about the different types of information is combined. The problem now is to explain the failures of overshadowing reported, for example, in Chapter 2.

7.4. Implications of Findings for Spatial Learning Based on Surface Boundaries

Recently, a similar point of view to that of Cheng’s (1986), has been expressed by Doeller and Burgess (2008; see also, Doeller, Kind, & Burgess, 2008). Basing their argument on findings from the performance of humans in a virtual maze, they suggested that learning about the significance of boundaries for finding a hidden goal will be unaffected by the presence of non-boundary cues that also signal where the goal is located. One supposition that Doeller and Burgess (2008) make is that there is a dual-system model of spatial learning. One system that is used in learning the direction and distance from surface

boundaries and the other one is used during learning the direction and distance from landmarks. The former is a specialised learning process that encodes information about where the goal is with reference to the boundaries of the apparatus, incidentally, while the latter occurs as a result of an associative process.

Doeller and Burgess (2008) found evidence that a landmark failed to overshadow and block learning the position of a goal with respect to the boundaries of the apparatus. An implication for these results is that the blocking effect demonstrated in Chapter 3 should not have been observed and at first sight, this finding to the contrary, appears to cast doubt on Doeller and Burgess. However, if the blocking effects that were reported in Chapter 3 were a consequence of attentional processes, rather than of an error-correcting learning algorithm (e.g., Rescorla and Wagner, 1972), then it may be possible to reconcile these results with the point of view that there is something special about spatial learning based on shape or boundaries. Perhaps learning about the position of a hidden goal with reference to boundaries does not compete with learning based on other cues and that effects such as blocking and overshadowing, when they occur, are a consequence of animals failing to pay heed to these cues because their attention is directed elsewhere. However, if in the experiments in Chapter 4, rats identified the position of the platform with reference to the boundaries created by distinctive shapes, then the fact that such learning was enhanced by the presence of an inhibitory landmark would strongly seem to pose a challenge to this proposal.

Another interesting result that Doeller and Burgess (2008) found was that although learning about a landmark failed to overshadow and block learning to find a goal with respect to surface boundaries, they clearly showed that learning the importance of surface boundaries overshadowed and blocked learning about landmarks. It then follows that the interaction between a surface-boundary dominated strategy and a landmark-based strategy interact in a competitive way. However this interaction was asymmetrical. That is, learning about surface

boundaries restricted learning about landmarks, but not vice versa. There is evidence to suggest, however, that the outcome may not be found with animals. McGregor, Horne, Ramos, and Pearce (in press) trained rats to find a submerged platform beneath a black spherical landmark in one corner of a triangular pool. Subsequent tests failed to reveal any evidence that the landmark overshadowed the geometric cues. However, McGregor et al., (in press) also failed to provide evidence for overshadowing learning about the landmark by geometric cues. Taken together, these results support the claim that learning about surface boundaries does not compete for control for spatial learning with landmarks, but, inconsistent with the claim by Doeller and Burgess that learning about surface boundaries restricts learning about landmarks.

Given both of the theories of spatial learning about geometric cues covered thus far (e.g., Cheng and Newcombe, 2005; Doeller and Burgess, 2008) it is fair to say that a specialised process of learning about geometric cues does not adequately explain the results of the current thesis and the results of past studies. The final theory to be discussed is one that is more simplistic in that it does not attempt to explain every result but provides yet another strategy that could be used by the rats in some instances.

7.5. Implications of Findings for View-Based Matching Accounts of Spatial Learning

Taking a completely different perspective on spatial learning in environments with a distinctive shape, Cheung, Stürzl, Zeil, and Cheng (2008; see also Stürzl, Cheung, Cheng, & Zeil, 2008) have proposed a view-based matching account of spatial navigation (e.g., Cartwright & Collett, 1983). They suggested that a reference, panoramic, image is taken at the goal location and the animal navigates on a current trial to minimise the difference between their current view of the environment and the reference image at the target location. It is implausible that rats are solely using a view-based matching system to navigate in all

environments given the results of this thesis. For example, the experiments in Chapter 2 failed to demonstrate overshadowing. In contrast, a view-based matching strategy would predict overshadowing because the panoramic image generated at the target location on training trials would include a landmark. During test trials with the landmark removed from the arena, it would be very difficult for the animal to find a view that accurately matches an image taken at the target location during training. This would presumably result in the animal performing poorly on the test trial compared to a group that received training without the landmark present.

Similarly, the demonstration of superconditioning in Chapter 4 also presents a problem for the view-based matching account of spatial learning. In these experiments, the last stage of training consisted of AX+ and AY+ trials for the superconditioning and control groups respectively (A represents the geometric cues; X and Y represent landmarks). The groups were then tested with only geometric cues present. If animals were using a view-based matching strategy then there would be no difference in performance of each group during test. Both groups would find it difficult to find an accurate match to the target location during training. The explanation for superconditioning relies on the difference between the groups in the previous reinforcement history of the landmark. A view-based matching strategy does not consider any prior reinforcement schedules.

According to Cheung et al. (2008), if one is testing a view-based matching account, then one would not also test for cue competition, and vice versa. This is because in a view-based matching account of spatial learning, “only one kind of cue, a panoramic image, is at play” (p. 28). Thus testing if multiple cues compete for the control they acquire over spatial behaviour would inherently provoke the use of an alternative strategy because multiple cues are expected to be used. Cheung et al. acknowledges the limitations of this view and suggests that this account is “a long way from showing that rats rely exclusively on a visual matching

strategy to navigate,” (p. 28), and most likely have a wide range of spatial strategies to use for navigating in environments with a distinctive shape.

As we have seen, a single model or theory cannot explain all the results in this thesis, although one based on a competitive learning rule (e.g., Rescorla and Wagner, 1978) does a far much better job than other theories, providing one acknowledges the influences of between-cue associations. This last point made by Cheung et al (2008), that animals have a number of spatial strategies to use whilst navigating may provide a good hint as to where research in this area is heading. The final section will extend this line of thinking.

7.6. Final Remarks and Future Directions

The empirical findings of this thesis add substantial theoretical insight to the area of spatial learning. It is clear from my findings that learning about geometric cues is not entirely void of associative principles as once thought (e.g., Cheng, 1986). Although there is substantial evidence to suggest that learning about geometric cues is governed by associative principles, it does not mean that there are not many overlapping mechanisms that may contribute to spatial learning in environments with a distinctive shape. This idea is not entirely without merit.

Recently, in another form of spatial learning it was suggested that the use of place and directional strategies occurs sequentially in a swimming pool task. On one hand, an animal that uses a place strategy locates a goal by using the relationship among an array of landmarks to pin point a specific place with reference to those cues. On the other hand, an animal using a directional strategy receives only orientation information from the array of landmarks and then heads off in a particular direction towards the goal. For example, Hamilton, Ackers, Johnson, Rice, Candelaria and Redhead (2009) trained rats for 12, 24 or 36 trials to locate a hidden platform located in a particular place in a pool with respect to

room cues and in a particular direction (e.g., North). For a test trial, the pool was translated 75 cm and time spent in two zones was recorded. The two zones corresponded to the location in the pool where the rats would be expected to go if they were using a place or directional strategy respectively. After only 12 training trials rats spent more time in the zone that corresponded to using a place strategy, however after 36 trials, rats spent more time in the zone that corresponded to using a directional strategy. Rats that were given 24 training trials showed no preference for either zone. This outcome suggested that multiple strategies are at play in this task and the use of such strategies follows a sort of hierarchy (Hamilton, Rosenfelt, & Whishaw, 2004; Maaswinkel & Whishaw, 1999). Since there is evidence of spatial hierarchies in some forms of spatial learning, such as the one described above, it is possible that such hierarchies are present while learning about geometric cues.

The basis of spatial hierarchies stems from the idea that there are separate modules governing different strategies (Shettleworth, 1998). Hamilton et al. (2004) trained rats with both distal landmarks and a beacon signalling the location of the platform. Using microanalysis of behaviour of each rat, it was observed that upon being released into the pool, rats made direct trajectories to the correct location. Shortly after the beginning of the trials, rats performed many horizontal head scans after which they would swim towards, and locate the platform. Removal of distal landmarks disrupted rats' initial trajectories to the platform but overall accuracy remained unchanged. However removal of the beacon left the initial trajectories unchanged but overall accuracy declined. Rats appeared to be using distal landmarks and the beacon sequentially. The same could be true for navigating in an environment with a distinctive shape. For instance, in the overshadowing experiments in Chapter 2, the experimental group was trained to locate a platform underneath a landmark in a corner of a triangular pool. Rats could have been using the geometric cues of the correct corner to gain their initial trajectories to the goal and the landmark could then be used to

provide fine grain place information as the rats get nearer the goal. In the control group, who received the same training except with the addition of an identical landmark in the opposite corner could also use this same strategy, thus no difference between the groups during performance on a test trial in the absence of any landmark would be expected.

It is hard to ignore the similarities between spatial hierarchies just described and serial conditioning in Pavlovian conditioning. Serial conditioning is a procedure in which two stimuli, A and B, are presented serially and then followed by a US. However, unlike serial conditioning where A is absent during the presentation of B, the geometric cues remain present when the rat has found the platform. If serial conditioning can be applied to spatial learning, it then implies that there is a shift of attention from geometric cues to the landmark as the trial progresses. In a case of serial conditioning where presentations of stimulus A is followed by stimulus B, which is then followed by the presentation of a shock ($A \rightarrow B \rightarrow \text{Shock}$), it has been shown that B potentiated, not overshadowed, learning about A when compared to a simple trace conditioning procedure ($AO \rightarrow \text{Shock}$; where O represents a trace interval prior to the administration of the shock) (Pearce, Nickolas, & Dickinson, 1981). Support of this result in the spatial domain can be taken from instances of potentiation of geometric cues in a kite-shaped swimming pool when two adjacent walls were black and the remaining walls were white (Graham et al., 2006; Pearce et al., 2006). This may provide an area for fruitful research in the future.

Another main finding from this thesis was that between-cue associations can form between geometric and non-geometric cues. These associations were speculated to be the cause for potentiation and the failure to find cue competition in the past, but no direct evidence for this exists. It is unclear how one would attempt to answer whether between-cue associations result in potentiation or compensate for overshadowing and blocking effects using behavioural means, but lesion work may provide the means to answer some of these

questions. Nicholson and Freeman (2000) conducted a sensory preconditioning experiment. For an experimental group of rats, the first stage consisted of non-reinforced pairings of a tone and light. In the second stage of the experiment only the light was reinforced. Following this training, conditioned responding to the tone was recorded. A control group was trained similarly except during the first stage of the experiment they received unpaired presentations of the tone and light. In normal rats, conditioned responding to the tone was greater in the experimental group than the control group, consistent with previous demonstrations of sensory preconditioning (e.g., Brogden, 1939). However, lesions of the perirhinal cortex completely abolished this effect. The most accepted explanation for sensory preconditioning is that during non-reinforced presentations of a compound stimulus, AB, a between-cue association develops between A and B (e.g., Rescorla and Cunningham, 1978). During reinforced trials of stimulus, A, the presence of A indirectly reinforces B via the between-cue association. Thus testing of B results in greater responding than a control group that did not receive explicit pairings of A and B. It then follows that the perirhinal cortex may be responsible for establishing between-cue associations between stimuli. If this outcome can generalise to spatial cues, then lesions of the perirhinal cortex may abolish potentiation of learning about geometric cues if potentiation is a direct result of between-cue associations forming between geometric and non-geometric cues. Similar experiments could be done to see if the past failures to find cue competition are a result of between-cue associations masking any overshadowing or blocking effects.

All of the present experiments looked at how learning of geometric cues is affected by the presence of landmarks. It appears that the interaction between geometry-based learning and landmark-based learning interact in ways predicted by the principles of associative learning given that superconditioning was found. This outcome is inconsistent with many theories that suggest a specialised learning mechanism for learning about geometric cues

(e.g., Cheng, 1986, Doeller and Burgess, 2008). However, it is also clear that a competitive learning rule, such as that described by Rescorla and Wagner (1972), is not the only mechanism at work during spatial learning in environments with a distinctive shape. Given the results of the blocking and overshadowing experiments, other mechanisms such as attention or spatial hierarchies may be influencing spatial learning. It remains for future research to determine the parameters contributing to animals using a competitive learning rule and the extent of influence that other spatial strategies may have on learning in an environment with a distinctive shape.

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