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AUSTEN, JOSEPH,MICHAEL

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An Analysis of Within-compound Associations in Spatial Learning

Joseph Michael Austen

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ABSTRACT

The nature of spatial learning has been argued to be qualitatively different from that of associative learning. Compelling evidence for this argument is provided by experiments showing a lack of typical associative cue-competition between spatial and non-spatial cues. However, this lack of cue-competition is also evident in wholly non-spatial experiments and has been explained by the presence of within-compound associations: an associative phenomenon. This thesis aims to determine whether such associations can explain similar cue-competition failures in spatial learning.

In a series of experiments it is shown that these within-compound associations exist between spatial and non-spatial cues in the rat, and that they can account for the frequent failure to observe typical cue-competition between these cues. In addition, it is demonstrated that the extent to which this failure occurs depends upon the relative salience of the cues in question.

In related experiments, it is also shown that these within-compound associations between spatial and non-spatial cues exist in humans. However, manifestation of these associations appears to depend on the gender of the participant, with associations forming in males but not in females. Further experiments suggest that this difference is likely due to the fact that the females are much less able to learn about the spatial cues in question.

It is argued that spatial learning need not be qualitatively different from associative learning if such associative phenomena as within-compound associations are accounted for.

DECLARATION

The work in this thesis is based on research carried out at the Department of Psychology, University of Durham, England, UK. No part of this thesis has been submitted elsewhere for any other degree or qualification and it is all my own work unless referenced to the contrary in the text.

PUBLICATION

The work presented in Chapter 2 has been published as follows:

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To Nic, a proper doctor.

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CHAPTER ONE

Introduction

Many species rely on an ability to form and store spatial information for their survival. Finding a food source, and remembering where it is so that it can be found again in the future, depends on an animal's ability to learn the spatial location of that food. In order to escape from a predator, an animal needs to be able to navigate from its current location to the safety of its home in the most efficient manner possible. To maximise its fitness, an animal may be required to navigate great distances to a mating site. It is therefore understandable that many animals have highly developed spatial abilities: those with the ability to learn where to eat, flee, and reproduce were more likely to propagate their superior genes.

Despite the importance of learning about spatial information, there is no consensus as to the mechanisms by which this learning occurs. Many have argued the mechanisms to be non-associative in nature, although more recently they are becoming better explained through associative principles. It is therefore of much disagreement whether spatial learning is associative or non-associative, and this argument has huge implications for the notion of a universal theory of learning. If spatial learning is qualitatively, rather than just quantitatively, different from learning in other modalities then such a universal learning theory appears unlikely.

Therefore, this thesis attempts to reconcile the domains of spatial and associative learning by demonstrating that spatial learning can be explained by reference to associative principles. Whilst many would argue that associative learning theories can explain aspects of spatial learning, there is still much contention over whether spatial learning is wholly associative in nature or warrants a unique and specialised theory of learning that is not fully compatible with that of an associative account. Associative learning prescribes no special status to cues of any modality and, as such, is internally compatible with learning of a spatial nature. Indeed, associative learning has been demonstrated within a wide variety of situations and across many species, from the nematode *Caenorhabditis elegans* (e.g., Rankin, 2000) to the adult human. It is therefore reasonable to expect that the rules governing associative learning also apply to spatial learning. However, there have been numerous claims against this viewpoint, the most vociferous of which are discussed in detail where appropriate. It is the purpose of this thesis to review the evidence for and against spatial learning being associative, and present a series of experiments to demonstrate that observations previously used as ammunition against an associative account of spatial learning can be readily explained in an associative manner.

1.1 Cognitive Map

That spatial learning may not follow the same fundamental principles as associative learning has been accepted since the term “cognitive map” was coined by Tolman (1948). This term has become widely used in the spatial cognition literature to refer to a high level of processing, possibly resulting in a representation being formed similar to that of a bird’s-eye view of the environment.

O'Keefe and Nadel (1978) presented a more rigorous definition of a cognitive map. They argued that it consists of two systems: a *place* system, and a *misplace* system. The place system holds information about places in the environment, objects in specific places within that environment, and the spatial relationships between these places and objects. The misplace system deals with changes in the environment, such as the introduction of a new object or the removal of an old one. With these two systems, animals are able to navigate within a familiar environment for which they have already generated a cognitive map, as well as explore a novel environment and generate a cognitive map in the process. Leonard and McNaughton (1990) stated, about cognitive maps, that "the essence of such a structure is the existence of a global representation of objects within some manifold or coordinate system from which their mutual spatial relationships can be derived" (p. 365).

The distinction between associative and spatial learning was exemplified by O’Keefe and Nadel (1978) who further defined two separate systems within the brain. The first of these systems, the locale system, was hippocampus-based and was required for learning about location. These locations were specified by the relationships between the various landmarks present, and different locations were linked together through exploration of the environment. The second of these systems, the taxon system, was instead concerned with route-following in the manner of stimulus-response learning.

This taxon system was thought to be extra-hippocampal and so physically separate from the locale system within the brain.

The theory of cognitive maps as a mechanism of spatial learning can be tested by examining the rules that govern spatial learning. If these rules fit with those under which associative learning is thought to occur, then a law of learning general to both spatial and non-spatial learning can begin to be formulated. One such rule of associative learning is cue competition, of which two examples are *overshadowing* and *blocking*. Overshadowing is the process by which the presence of more than one stimulus signalling an outcome causes each stimulus to be less well learned about than if the outcome were predicted by only one of the stimuli alone (Pavlov, 1927). For example, if two stimuli, *A* and *B*, both signal an outcome then less will be learned about the relationship between *A* and the outcome than if *A* were trained to signal the outcome in the absence of *B*. In this instance, the presence of *B* would be said to have overshadowed learning about the importance of *A*. In addition, the presence of *A* would restrict the amount learned about *B*, when compared with training that involved the outcome being signalled by *B* alone. Blocking refers to an inability to learn the relationship between a stimulus and an outcome when that stimulus is presented as part of a compound that contains another stimulus that has previously been paired with the outcome (Kamin, 1969). For example, if a stimulus, *A*, is trained to signal an outcome, and then that stimulus is paired with another stimulus, *B*, and trained to signal the same outcome, little will be learned about the relationship between *B* and the outcome. In this case, the prior learning about *A* is said to have blocked learning about *B*.

Associative learning and cognitive maps make difference predictions for several spatial learning scenarios. This allows an examination of which of these theories is the most likely mechanism by which spatial learning operates. One property of cognitive maps, according to O’Keefe and Nadel (1978), is that the addition of new features to a map should occur rapidly and without interference from any features already held within the map. This implies that if animals have already learned about the location of a goal with respect to certain features, they will be able to learn its location with respect to the newly added features just as rapidly as if the initial features had not been learned. In other words, learning about spatial information should not be susceptible to blocking. However, many demonstrations of blocking in the spatial domain have been shown (e.g., Biegler & Morris, 1999; Diez-Chamizo, Sterio, & Mackintosh, 1985; Hamilton & Sutherland, 1999; Redhead, Roberts, Good, & Pearce, 1997; Roberts & Pearce, 1999; Rodrigo, Chamizo, McLaren, & Mackintosh, 1997), and these findings can all be explained by appealing to an associative account of spatial learning, rather than a cognitive map system.

Another property of cognitive maps is that a landmark that does not maintain a static relationship with other aspects of the environment, that is it moves around within the environment, will not be learned about. This derives from the idea that the features of a map should be stable in order to maximise the usefulness of that map. However, Roberts and Pearce (1998) demonstrated that animals can learn the relationship between a landmark that moves around within its environment and a hidden goal that remains at a constant position in relation to that landmark. This goes counter to the predictions of a cognitive map, but can be adequately explain associatively by appreciating that an association forms between the position of the landmark and the location of the goal and that this association is constant, despite both landmark and goal being unstable with respect to the rest of the environment.

Despite the evidence detailed above that cognitive maps do not account for the learning evident within certain scenarios of spatial learning, they remain a mechanism for spatial learning with certain merit and considerable support. Gallistel (1990) stated that a cognitive map should be "a record in the central nervous system of macroscopic geometric relations among surfaces in the environment used to plan movements through the environment" (p. 103). The rules under which these geometric relations are learned are thought to be exemplified by the geometric module experiments of Cheng (1986).

1.2 Geometric Module

Cheng (1986) and Gallistel (1990) proposed that there was a geometric module within the brain that was responsible for learning about the geometric relationships within an environment. Empirical evidence for the presence of this dedicated geometric module was initially demonstrated by Cheng (1986). He released rats into a rectangular arena, with distinctive featural cues in each corner. Food was buried within the arena, and the rats had to search the environment until they found the location of the food reward. After eating a small amount of the reward, the rats were then removed from the arena, disorientated, and placed back inside the arena to relocate the food, which had been reburied. Despite the presence of the featural cues, which served to disambiguate all four corners of the rectangle, the rats searched for the reburied food as though they were only using the geometric cues provided by the rectangular shape of the arena. There was no difference between the time spent searching for the food in the correct location and the time spent searching in a location that was also correct with respect to the shape of the arena, but incorrect with reference to the disambiguating featural cues. These results were observed despite the featural cues being not just visually distinct, but also differing in their lighting, texture, and odour. In fact, the same pattern of results was evident when one entire wall of the rectangular arena was a different colour to the rest. Even in the presence of such an obvious featural cue, the rats appeared to be learning based solely on the geometric properties of the rectangular arena. A further experiment demonstrated that with increased training, the rats could learn to disambiguate the geometric cues by reference to the discriminable featural cues. However, Cheng argued that the animals did not use the overall arrangement of the featural cues to locate the buried food, but instead used primarily the geometric cues and then checked whether the featural cue at this location matched with the featural cue observed previously. Furthermore, he asserted that these featural cues were pasted on to the framework of geometric cues after extended training, but that both geometric and featural cues were learned independently of one another.

Gallistel (1990) argued that there was theoretical justification for such a geometric module being impenetrable to non-geometric information. This argument was based on the changing nature of non-geometric cues, such as landmarks within an environment, compared with the relatively static nature of the shape of an environment. If animals paid too much attention to these changing non-geometric cues, then navigation through a familiar environment during a time when these non-geometric cues may have changed, for example during winter, would be affected. If, on the other hand, animals had learned to navigate with respect to the stable geometric properties of the environment, and learned little about the changing non-geometric features, navigation through such a featurally-changed environment would not present the same difficulty.

As Cheng (1986) argued that learning about the geometric and featural cues of an environment occurs independently of one another, it can be inferred that these cues should not interact in the manners predicted by associative learning. For example, neither overshadowing nor blocking of geometric cues by landmark cues should occur. However, the results of Cheng’s experiments do not preclude the influence of associative phenomena. It was discussed earlier how the presentation of two cues in compound results in each cue overshadowing learning about the other, when compared with learning based on each cue presented alone. Cheng’s animals were presented with both geometric and featural cues indicating the location of a hidden food reward and so associative theories would readily predict overshadowing between these two cues. It is conceivable that the reason animals learned little about the featural cues of the environment was because the geometry cues were of relatively higher salience and overshadowed learning about the non-geometric cues. This overshadowing, while giving the same pattern of results as Cheng observed, goes counter to the argument that learning about geometric and non-geometric cues progresses independently. In addition, it is possible that learning about the geometric cues was overshadowed somewhat by the presence of the discriminable featural cues. An appropriate control group, demonstrating learning about geometric cues in the absence of the featural cues, would have demonstrated the presence or absence of such overshadowing, but was not included in Cheng's experiments.

In light of Cheng's (1986) failure to provide convincing evidence of a lack of associative rules by demonstrating that overshadowing had not occurred between his geometric and non-geometric cues, Pearce, Graham, Good, Jones, and McGregor (2006) conducted an experiment to determine whether featural information was able to restrict learning about geometric cues. Two groups of rats were trained to locate a hidden platform in one corner of a rectangular water maze. For one of these groups, all four of the walls of the arena were white and so rats were able to locate the platform based solely on the shape of the arena. For the other group, two adjacent walls of the arena were black, and the other two walls white. This group of animals could therefore locate the platform with reference to either the shape of the arena, or the colours of the arena's walls. After training, both groups of animals received a single test trial in a rectangular arena with four white walls, and in the absence of the escape platform. Associative learning theories would predict that the presence of the discriminable wall colours for one of the groups of animals should restrict how much that group learned about the geometric cues. Therefore, when tested with only the geometric cues present, when all four walls were the same colour, this group of animals should discriminate less readily between the geometric cues than the group of animals trained to locate the platform by reference to only the geometric cues throughout training. This is exactly the result that Pearce et al. observed: the presence of discriminable wall colours during training restricted the amount learned about the geometric cues. This is problematic for the proposal by Cheng (1986) and Gallistel (1990) that learning about geometric cues progresses independently of learning about non-geometric cues.

It could be argued that the independence of geometric and non-geometric learning, as a consequence of the dedicated geometric module proposed by Cheng (1986) and Gallistel (1990), is dependent on the non-geometric cues not being integrated within the geometric cues. The non-geometric cues used by Pearce et al. (2006) to demonstrate overshadowing of geometric learning were the colours of the walls of the arena. This non-geometric cue is closely integrated with the geometric cue, and it may have been able to access the geometric module, and compete with the geometric cues, for this reason. However, the geometric module theory would certainly not permit non-geometric cues completely separate from the geometric cues, such as discrete landmarks, to enter into competition with the geometry. Several experiments appear to concur with such an argument, with discrete landmarks failing to block or overshadow learning about geometric cues (Hayward, Good, & Pearce, 2004; Hayward, McGregor, Good, & Pearce, 2003; Kelly, Spetch, & Heth, 1998; McGregor, Horne, Esber, & Pearce, 2009; Pearce, Ward-Robinson, Good, Fussell, & Aydin, 2001; Wall, Botly, Black, & Shettleworth, 2004). These failures to demonstrate overshadowing or blocking are not consistent with the associative theories as explained earlier, but this need not be unequivocal evidence for the presence of a geometric module impenetrable to non-geometric cues, as will be discussed further. In addition, recent work has shown that discrete landmarks cues are able to restrict learning about geometric cues under certain circumstances (Kosaki, Austen, & McGregor, 2013). This demonstration presents strong opposition to the theory that a geometric module does not allow interaction between geometric and non-geometric cues. Conversely, traditional associative theories encounter no difficulties explaining such overshadowing effects.

More recently, Doeller and Burgess (2008) have proposed, in a manner similar to Cheng (1986) and Gallistel (1990), that learning about landmarks and geometry (by which they mean the boundary of an environment) progress independently from one another. This would appear to provide evidence for cognitive map theory, which would predict a lack of competition between these cues, whilst contradicting the predictions of an associative theory of spatial learning, which would argue that landmarks and boundaries should interact and compete for learning. However, a closer analysis of their experiments would suggest that Doeller and Burgess do not provide strong evidence for spatial learning progressing in a non-associative manner. Their evidence for this assertion comes from a series of experiments looking at cue competition and blocking between landmarks and boundaries. Two groups of humans were trained to remember the locations of certain objects in a virtual environment. One group could learn these object locations based on the presence of a single landmark cue with polarising cues in the distance. Another group was able to use this landmark cue and a circular boundary surrounding the environment, with the same polarising cues present. After training, both of these groups were tested with only the landmark cue present, to determine how much they had learned about the locations of the objects with reference to this landmark cue. Unsurprisingly, the group trained with only the landmark cue present throughout training had learned more about the relevance of this landmark cue than those trained with both the landmark cue and the boundary cues: the presence of the boundary cues had overshadowed learning about the landmark cue. However, the results of two more groups do not agree so readily with associative theory. One of these groups was trained with a compound of landmark and boundary cues, with polarising cues, as before. The other group was trained with only the boundary and polarising cues present. After training, these two groups were tested on how much they had learned about the location of the objects with reference to only the boundary cues. In this experiment, the two groups showed similar learning about the boundary cues. The presence of the landmark cue had not restricted how much had been learned about the boundary. This led Doeller and Burgess to the conclusion that learning about landmark and boundary cues progressed independently, and that boundary cue learning was not influenced by the presence of landmark cues.

However, their experiments were confounded by different levels of generalization decrement between the groups. For the group trained with only landmarks, and then tested with only landmarks, the training and test situations were very similar. This group therefore suffered very little generalization decrement in the test trials. However, the performance of this group was compared with one in which training with both landmark and boundary cues was followed by testing with only landmark cues. The removal of the boundary cues, which in this case were a circular mound surrounding the arena and large mountains in the distance, meant that the training and test situations were very different for this group. Their poorer performance could therefore be readily attributed to this greater generalization decrement, rather than overshadowing of the landmark cues by the boundary. Without proper control conditions, it is impossible to determine whether the boundary cues did restrict learning about the landmark cues in their experiment. The fact that their second experiment was also hampered by this lack of a sufficient control group goes even further to discredit their claims that boundaries and landmarks affect learning about one another to differing degrees. In this experiment, as described, both groups were tested with only boundary cues. Therefore, the group trained with only boundary cues experienced very little generalization decrement between training and test. However, the group trained with landmarks and boundary cues experienced a greater level of generalization decrement. Without this generalization decrement, it may well have been observed that the presence of landmark cues did affect learning based on the boundaries, an outcome consistent with the predictions of associative theory.

Had generalization decrement been satisfactorily accounted for, it may still be no surprise to observe asymmetrical overshadowing in a study such as that by Doeller and Burgess (2008). Mackintosh (1976) would predict such asymmetrical overshadowing depending on the associability of the cues involved, which depends on their salience. In Doeller and Burgess, if the boundary was a more salient cue than the landmark, it would be expected that the boundary would overshadow learning about the landmark. However, it would be no surprise if the less salient landmark cue did not restrict learning about the boundary. That asymmetrical overshadowing is observed does not require learning about the cues to occur independently, only for the cues to differ in salience.

1.3 Associative Spatial Learning

Despite the prevailing discussion, which demonstrates that associative learning is able to account for much of spatial learning, there remain situations in which associative learning does not adequately account for observed phenomena. If properly controlled experiments concurred with the results of Doeller and Burgess (2008), then it could be convincingly argued that landmark cues are unable to overshadow learning about boundaries in humans. In addition, there are numerous studies that fail to demonstrate overshadowing of geometry cues by non-geometric features of the environment (Hayward et al., 2003; Hayward et al., 2004; McGregor et al., 2009; Pearce et al., 2001; Wall et al., 2004). There are still others that demonstrate enhanced learning, or potentiation, of geometric cues via concurrent training with landmark cues (Cole, Gibson, Pollack, & Yates, 2011; Graham, Good, McGregor, & Pearce, 2006, Horne & Pearce 2011; Pearce et al., 2006). These results would all be difficult for associative theories, in the form presented earlier, to account for.

1.3.1 Miller and Shettleworth (2007)

One attempt to reconcile those results described above with associative theories was presented by Miller and Shettleworth (2007). Contrary to a number of theories (Cheng, 1986; Doeller & Burgess, 2008; Doeller, King, & Burgess, 2008; Gallistel, 1990; Wang & Spelke, 2002, 2003), Miller and Shettleworth do not ascribe any special status to learning about geometric cues. Instead, they argue that a modified version of the Rescorla and Wagner (1972) equation can account for failures of overshadowing of geometric cues by landmarks. Their theory accounts for the probability that a certain corner will be visited upon release into an arena, with the probability being calculated by dividing the associative strength of the corner in question by the sum of the associative strengths of all of the corners present within the arena. This probability is then multiplied by the result from the standard Rescorla-Wagner equation to determine the change in associative strength of each corner as a function of the probability of that corner being entered. With the addition of this probability rule, animals no longer experience each cue equally during each trial, as would be the case in standard overshadowing designs in Pavlovian conditioning. It is the presence of a landmark above certain corners that increases the probability of entering that corner, through a process Miller and Shettleworth termed feature enhancement, and it is through this mechanism that landmarks can fail to overshadow, or even potentiate, learning about geometry.

The model of associative learning put forward by Miller and Shettleworth (2007) can adequately explain the lack of cue competition and potentiation of geometry cues by landmarks in various experiments by Graham et al. (2006), Pearce et al. (2001), and Pearce et al. (2006). However, not all failures to overshadow one cue by another can be explained quite so readily. McGregor et al. (2009) conducted two experiments that failed to demonstrate overshadowing between geometry and discrete landmark cues. Modelling these experiments using the associative theory provided by Miller and Shettleworth predicted that overshadowing would occur in both situations. This would suggest that either Miller and Shettleworth’s associative model is not the reason for the frequently observed overshadowing failures, or that it is only able to account for a subset of these failures (see also Horne & Pearce, 2009b; Horne & Pearce, 2010). Whichever of these is true, it is clear that there are other factors involved in the absence of overshadowing between spatial cues.

1.3.2 Within-Compound Associations

In an attempt to overcome the potential problems faced by associative theory in the spatial domain, the application of associative theory to other modalities can be consulted. Potentiation, the enhancement of learning about one cue as a consequence of it being trained in compound with another cue, has been demonstrated in non-spatial studies. For example, Clarke, Westbrook, and Irwin (1979) administered toxin to pigeons following exposure to certain cues. One group of pigeons received toxin after drinking a distinctively coloured solution with a novel taste. Another group received toxin following consumption of a coloured, but tasteless, solution. Clarke et al. observed a stronger aversion to the coloured liquid from that group of pigeons trained with a compound of coloured liquid and taste. Whereas traditional associative theories would predict overshadowing of the coloured liquid by the presence of the taste, potentiation was observed. This is not an isolated example, with Galef and Osbourne (1978) reporting a similar result in rats, and Rusiniak, Hankins, Garcia, and Brett (1979) demonstrating potentiation of aversion to an odour by pairing it with a taste cue.

Rusiniak et al. (1979) argued that the association between the odour cue and the aversion was facilitated by the presence of the taste cue. This argument is not compatible with the associative theories that could explain overshadowing, as those theories would predict competition between cues, rather than facilitation. This led Rusiniak et al. to conclude that theories of associative learning were not applicable to the results of flavour-aversion experiments. However, Durlach and Rescorla (1980) provided an explanation for these results in accordance with associative theory. They administered lithium chloride (LiCl) toxin to rats following consumption of water containing certain cues. For one group of animals this water contained only an odour cue, and for the other group it contained both odour and taste cues. It was observed that aversion to the odour was greater for the group that was trained with a compound of odour and taste cues prior to receiving the toxin. Durlach and Rescorla argued that the presence of the taste cue did not facilitate the association between the odour cue and the toxin, as asserted by Rusiniak et al., but that during training the odour and taste cues became associated together; that is, a within-compound association formed between the two stimuli. The aversiveness to the odour cue trained alone can be thought to be a consequence of the association between that odour and the toxin. However, the aversiveness of the odour cue trained in compound with the taste cue was a combination of the association between the odour cue and the toxin, in addition to the association between the odour cue and the taste cue. During training it is likely that this taste cue became aversive in its own right, having been consistently paired with toxin. Therefore, the total aversiveness to the odour for the group trained with a compound of taste and odour cues was higher than that for those trained with the odour cues alone.

The work of Durlach and Rescorla (1980) in explaining potentiation within an associative learning framework potentially holds the key for understanding such effects within the spatial domain. If such within-compound associations could be observed between spatial cues then it is possible to explain associatively those cue competition phenomena that are claimed, in a manner akin to Rusiniak et al. (1979), to be governed by non-associative principles. Therefore, the following series of experiments seeks to determine whether the presence of within-compound associations can account for the apparent absence of cue-competition observed. Through this, it is hoped that spatial learning can be seen to follow the same rules that govern learning in other modalities. This is an important step towards the formation of a unified theory of learning.

1.4 Anatomy of the Thesis

Chapter 2 aims to provide a demonstration of the potentiation of geometry learning via training in compound with landmark cues. In an attempt to avoid the argument that any cue-competition is the result of landmark cues being able to enter the geometric module, these landmarks will be spatially and visually discrete from the geometric cues. The influence of within-compound associations between these landmark and geometry cues will then be tested, and their involvement in cue-competition effects discussed.

Chapter 3 will broaden the conclusions of Chapter 2 by investigating whether geometric cues are able to restrict or enhance learning about landmark cues. This will further the evidence that the learning between these cues proceeds in an associative manner. In addition, the role of within-compound associations in these cue-competition effects will be addressed.

Chapter 4 aims to present a generalisation of the presence of within-compound associations in spatial learning to human participants. Additionally, the effect of the participant's gender on the presence or absence of these associations will be determined.

Chapter 5 will explain the source of the gender difference uncovered by the experiments of Chapter 4. Evidence against one theory behind these gender differences (ability to switch strategies at different rates) and for an alternative theory (that the different genders learn more readily about different types of cue) provides further support for an associative account of spatial learning.

Chapter 6 presents a summary of the most pertinent conclusions from Chapters 2-5, and provides a discourse on the evidence for spatial learning being associative in nature.

CHAPTER TWO

Landmarks Potentiate Learning About Geometry

When two or more cues signal the same outcome, theories of associative learning most commonly predict that learning based on one of the cues will restrict learning based on the others (e.g., Pearce, 1994; Rescorla & Wagner, 1972). Although these theories of associative learning have been applied to conditions under which Pavlovian conditioning progresses, they do not specify the type of learning that the theory can explain, and are therefore considered to constitute general learning rules. Spatial learning might therefore be considered to follow the same general rules as Pavlovian conditioning. Examples of associative phenomena, such as pre-exposure effects, latent inhibition, and cue competition effects, such as overshadowing and blocking, have all been demonstrated in experiments in which an animal has to navigate to the location of a hidden goal (e.g., Diez-Chamizo et al., 1985; Prados, Redhead, & Pearce, 1999; Roberts & Pearce, 1999, review in Chamizo, 2003).

Although there are demonstrations of cue competition in spatial learning, there are circumstances under which failure to demonstrate cue competition is common. The best-documented example of such a case is when an animal has to learn the location of a hidden goal with reference to the shape of the environment. Many studies have demonstrated the ability of a variety of animals to use the geometric properties of the environment for navigation; examples include rats (e.g., Cheng, 1986), mice (e.g., Fellini, Schachner, & Morellini, 2006), birds (e.g., Vallortigara, Zanforlin, & Pasti, 1990), fish (e.g., Sovrano, Bisazza, & Vallortigara, 2002), monkeys (e.g., Gouteux, Thinus-Blanc, & Vauclair, 2001), and humans (e.g., Hermer & Spelke, 1996; Ratliff & Newcombe, 2005). When cues in addition to the geometry also indicate the goal's location it might be supposed, from the foregoing discussion about the associative nature of spatial learning, that these cues will restrict the amount learned about the geometry. However, a number of studies using a variety of species have failed to provide a consistent set of results when the cues trained in concert with geometric cues are of a non-geometric nature. Non-geometric cues have been previously defined as those cues that are not based on geometric relationships between the shape of the environment and the location of the goal, with examples including featural information from surfaces, such as wall color, and discrete objects within the environment. Often there was no evidence that additional non-geometric cues could restrict learning based on geometry (Hayward et al., 2003; Hayward et al., 2004; McGregor et al., 2009; Pearce et al., 2001; Wall et al., 2004). Such evidence has been taken to support the notion that animals formed a representation of environmental geometry in a dedicated module that was impervious to the effects of learning based on non-geometric features (Cheng, 1986; Gallistel, 1990).

However, in some studies, when both the geometry of the arena and the color of its walls indicated the location of the goal, learning based on the geometry was disrupted by concurrent learning based on the wall color (Cole et al., 2011; Gray, Bloomfield, Ferrey, Spetch, & Sturdy, 2005; Pearce et al., 2006). McGregor et al. (2009) suggested that non-geometric cues of this type might be integrated into a representation of geometry in a way not possible for discrete landmarks, although they argued such a proposal would lay open to question the validity of a purely geometric module for spatial learning. More recently, however, some studies have revealed evidence of the ability of discrete landmarks to compete for control over behavior with geometric cues (Horne & Pearce, 2009a; Kosaki et al., 2013). Kosaki et al.'s results were particularly important because they identified the conditions under which overshadowing of geometry by landmarks should occur. In their Experiment 2 they trained rats to locate a platform in one of the two acute corners of a rhombus shaped pool. In addition to the geometric cues provided by the pool's shape, a landmark was always suspended over the platform, but not over the opposite acute corner. Thus, the landmark was a more valid predictor of the platform's location than the geometry. Another group was trained in a similar way but with the platform always located in one of the two obtuse corners. In a test trial the landmark and platform were removed from the pool and the time spent searching for the platform in the different corners of the pool was recorded. The performances of these overshadowing groups were compared with those of two control groups, one trained to locate the platform in one of the two acute corners and the other trained to one of the two obtuse corners. These control groups were trained in a similar way to their respective overshadowing groups but with a landmark suspended over each of the four corners of the pool. The control groups were expected to learn the significance of the geometric properties of the corner in which the platform was located to a greater extent than the overshadowing groups, for which the landmark was a more valid cue for locating the platform. The higher validity of the landmark resulted in overshadowing regardless of the angle of the corner. In a further experiment, Kosaki et al. controlled for differences in the relative validities of the landmarks and geometry between the overshadowing and control groups, and showed that the landmarks were only able to overshadow geometry for those animals trained to locate the platform in the obtuse corner, which they argued was of a lower salience than the acute corner. Therefore, the relative salience of the landmark cues in compound with the geometry is an important factor in determining the extent to which overshadowing of geometry can occur, in addition to differences in the relative validities of landmarks and geometry.

Although differences in relative validity and salience may offer an explanation for the frequent lack of overshadowing or blocking of geometry by landmarks, these differences are less able to explain the observation that learning based on non-geometric cues can enhance performance based on geometry (Cole et al., 2011; Graham et al., 2006, Horne & Pearce, 2011; Pearce et al., 2006). This improvement in learning about one cue when trained in the presence of another cue is known as potentiation, and such an effect contradicts those theories of associative learning that utilize a global error term to predict that cues compete for control over behavior. As such, understanding the conditions under which potentiation occurs may allow us to determine the generality of associative learning principles with respect to spatial learning.

One theory put forward to explain these potentiation results is that of within-compound associations. Pearce et al. (2006) argued that during water maze training with a compound of geometric and non-geometric cues, the non-geometric cue entered not only into a direct association with the platform, but also into an association with the geometric cue with which it was paired. When animals were then tested in the absence of the platform and the non-geometric cue, the presence of the geometric cue associated with the platform should activate a memory of the non-geometric cue with which it was paired during training. This evokes a representation of the association between the non-geometric cue and the platform, which should enhance responding to the geometrically correct location. If the within-compound association is able to evoke a representation of the non-geometric cue, then any overshadowing of the geometry by this non-geometric cue may be counteracted by the boost in performance afforded through the within-compound association. Such an explanation can account for the lack of overshadowing of geometry by non-geometric cues in a variety of studies (e.g., Hayward et al., 2003; McGregor et al., 2009; Pearce et al., 2001). If the evoked representation of the non-geometric cue is particularly strong, then any overshadowing may be more than compensated for by this boost in performance, resulting in enhanced responding to the geometric cues (i.e., potentiation).

Direct evidence of the existence of these within-compound associations comes from an experiment by Horne and Pearce (2009b) in which rats were trained to locate a platform in a pool with reference to cues provided by its distinctive shape in addition to non-geometric cues provided by the colors of the arena's walls. Following training with reference only to the wall colors, during which the value of the wall colors was reversed, the rats lost their discrimination of the correct and incorrect geometric corners when tested with only the distinctive shape. Rats in a control group that received training with the wall colors that was consistent with their original training showed no such loss of discrimination. Rhodes, Creighton, Killcross, Good, and Honey (2009) extended the generality of this finding to an appetitive task. In their analysis of the circumstances under which potentiation and overshadowing of geometry learning occurred, Horne and Pearce (2011) proposed that the extent to which the non-geometric cue should overshadow the geometry is modulated by its salience. A salient non-geometric cue should overshadow geometry strongly, such that the within-compound association cannot compensate for this effect, which results in an overall overshadowing effect. Conversely, with a less salient non-geometric cue, the overshadowing effect should be weaker, such that it may be more than compensated for by the indirect association between the non-geometric cue and the platform, resulting in potentiation being observed. Although their results were consistent with an explanation based on within-compound associations, Horne and Pearce (2011) did not assess directly the extent to which within-compound associations were responsible for such an effect.

The purpose of the current chapter is to determine whether the frequently observed failure of discrete landmarks to overshadow learning based on geometry is the result of within-compound associations between the landmark and the geometry. It sought to test the generality of Horne and Pearce’s (2011) analysis of the circumstances in which overshadowing and potentiation will occur to similar situations with discrete landmarks. Accordingly, in Experiment 1 the relative saliences of two discrete landmarks were examined. In Experiment 2 it was predicted that overshadowing would be less apparent for the group trained with the landmark established in Experiment 1 as the less salient cue. The results of Experiment 2 confirmed that the less salient landmark potentiated geometry, but that, as McGregor et al. (2009) found after using a similar landmark, animals trained with the more salient landmark showed neither overshadowing nor potentiation. In Experiment 3 it was determined if within-compound associations had formed between the landmark and geometric cues used in Experiments 1 and 2.

2.1 Experiment 1

When two cues are trained in compound to signal an outcome, the strength of the association formed between each cue and the outcome after a given number of trials is assumed to be proportional to the salience of the cues (Rescorla & Wagner, 1972). To assess the relative saliences of the two different landmarks, a comparison was made of the control they acquired after being trained, in conjunction with geometric cues, to indicate the location of the hidden platform. Rats were trained to locate a submerged platform in one of the two base corners of an isosceles triangular-shaped arena, with the base wall created by the curved wall of the circular water maze. The rats were additionally presented with two different landmarks, one placed directly over each of the two base corners of the triangle. Following this compound training a single test trial was given in which the two landmarks were presented in the absence of the geometric cues provided by the arena. Animals should discriminate between the two landmarks more readily when the more salient landmark indicates the location of the hidden platform.

2.1.1 Method

2.1.1.1 Subjects

The subjects were ten male Lister Hooded rats (*Rattus norvegicus*) supplied by Harlan Olac (Bicester, Oxfordshire, England). They were approximately nine weeks old at the start of testing, were tested for a total of six weeks, and were not used in any other study before the experiment began. The animals were housed in pairs in cages in which they had continuous access to food and water. These cages were in a light-tight holding room on a 12 h light:dark cycle, with lights coming on at 8:00 am. The animals were always tested when the lights were on in their holding room, and at a similar time each day.

2.1.1.2 Apparatus

A white fiberglass Morris water maze, with a diameter of 2 m and a depth of 60 cm, was mounted on a wooden platform 40 cm above the floor. Each day, the water maze was filled to a depth of 30 cm with water (25 ± 2 °C) to which was added 500 ml of white opacifier (OP 303B; Rohm & Haas, Dewsbury, England). After testing, the pool was drained and cleaned along with all other apparatus in contact with animals. The pool was fully surrounded by an opaque grey curtain which prevented the animals being able to utilize any visual extra-maze cues. This curtain fell 25 cm from the rim of the water maze and extended from the ceiling to 25 cm beneath the top of the water maze. Suspended directly above the pool, at a height of 1 m above the top of the walls, was a white circular polyurethane sheet, 2 m in diameter. This artificial ceiling contained eight 45 W spotlights (each 22.5 cm in diameter) arranged in a circular array with a diameter of 1 m, centered within the circular artificial ceiling. These spotlights illuminated the pool throughout the experiment. A 30 cm diameter circular hole in the center of this array allowed a wide-angled video camera, which was set 5 cm above the artificial ceiling, to relay an image of the water maze to a monitor, recording equipment, and a PC in the north-east corner of the room. Tracking software (EthoVision, Noldus, NL) was used to record the rats’ swim paths during the experiment. The pool, curtains and artificial ceiling were situated in the approximate center of a room with dimensions 4.65 x 3.90 x 2.25 m high, with a door situated in the north 3.90 m wall. This room was illuminated by two strip lights (each 35 W), one attached to each of the long walls of the experimental room. These strip lights were 150 cm long and affixed 68 cm horizontally above, and parallel to, the floor.

To create a triangular-shaped arena within the circular water maze, two polyurethane boards, 180 cm in length, 59 cm high and 0.5 cm thick, were attached to square lengths of aluminium tubing (1.2 cm square cross-section), which extended 10 cm further than either end of the polyurethane boards in order to suspend the boards within the pool by resting the aluminium tubing on the top edge of the water maze. The third wall of the triangular-shaped arena was formed from the curved wall of the circular water maze. In the landmark test at the end of training there were no polyurethane walls present and the entire circular water maze was used with the landmarks presented in diametrically opposite quadrants of the pool. The landmarks were suspended from thin white wires attached to the artificial ceiling such that the distance from the center of each landmark to the surface of the pool was 30 cm. These two landmarks were placed on an imaginary line that bisected the arena in a south-west to north-east direction. One landmark was suspended 63 cm from the south-west edge of the water maze and the other 63 cm from the north-east edge.

During training, a circular Perspex platform, with diameter 10 cm, was submerged at a depth of 2 cm below the surface of the water. The surface of this platform consisted of concentric circular grooves to increase traction. Two landmarks were used in this study. One was a dense sponge ball, 9.5 cm in diameter, painted matte black. The other was a hollow octagonal prism, the inside and outside of which was painted white. The eight walls forming this prism were 9.5 cm tall, 4 cm wide, and 1 cm thick. A 5 mm-thick grey Perspex lid covered the top of the prism. The bottom of the prism remained open, with the exposed edges painted black. Two black stripes were painted horizontally around the center of the prism, each being 2.5 cm wide, with a 1 cm gap separating them. Both the ball and prism landmarks were suspended such that the center of each was 30 cm above the surface of the water. This was achieved by attaching each landmark to 8 mm diameter Perspex rods, which were attached horizontally to the aluminium tubing suspending the polyurethane walls. The landmarks were placed at a distance of 25 cm from the base corners of the triangular arena that were made up from one straight wall and the curved base, on a line bisecting each corner. Depending on the training condition, the platform was placed directly underneath one, or other, of the landmarks. A schematic of the arenas used for each phase of this experiment can be seen in Figure 2.1

2.1.1.3 Procedure

At the beginning of the experiment the ten animals were split randomly into two similar groups based on the landmark beneath which the platform was located during compound training. Half of the animals always found the platform underneath the ball landmark (Group Ball), with the other half locating it underneath the prism landmark (Group Prism). It was not possible to fully counterbalance the corners in which the rats located the platform, so within each of the two groups, three animals were trained to find the hidden platform in one of the base corners of the triangle, with the straight wall to the left of the curved wall, with the other two animals in each group finding the hidden platform in the other base corner, which had the opposite arrangement of walls (see Figure 2.1). Across the two landmark groups, equal numbers of animals found the platform in each of the two base corners of the arena. The non-reinforced landmark was always present in the base corner that did not contain the platform during training. The platform could be located using the distinct shape of the arena, and also by discriminating between the landmarks.

At the beginning of a session, rats were transported in squads of five to the experimental room in separate compartments of a light-tight carrying box. This box was

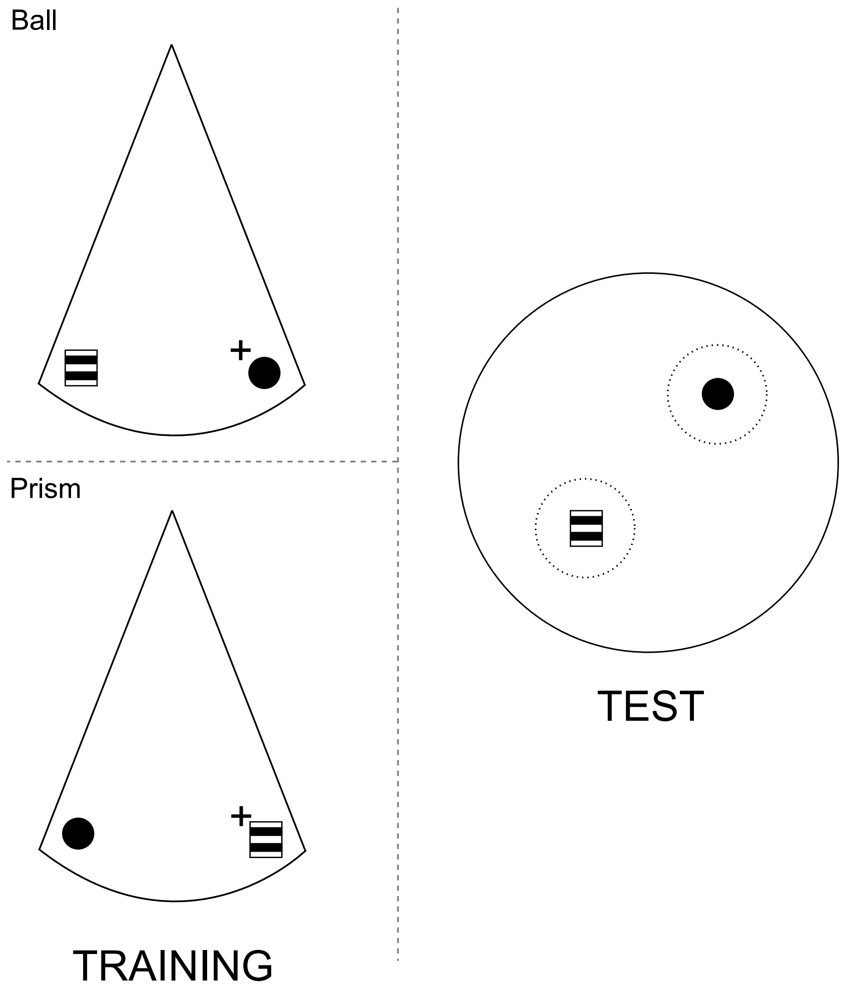


Figure 2.1: Procedure used in Experiment 1 to determine relative saliences of the ball and prism landmarks when trained in compound with geometry. Filled black circles represent the ball landmark, horizontally striped squares represent the prism landmark, '+' signs denote the landmark under which the hidden escape platform is located, and the dotted areas denote the areas in which exploration times during the test trial are queried.

placed onto a table in the north-west corner of the room. During training a rat was removed from the carrying box and placed into the water maze at the center of one of the three walls, facing the wall. The rat swam until it located the platform, after which it was allowed to remain on the platform for 20 s until it was removed from the pool by the experimenter, dried, and returned to the carrying box for an inter-trial interval of approximately 5 minutes. If an animal failed to locate the platform within 60 s it was guided there by the experimenter. No training was required for the rat to follow the experimenter’s hand. Animals received four trials per session, over the course of 18 sessions, with a single session per day. Throughout training, the curtains were drawn around the pool such that the animals were unable to use any cues beyond the curtain to locate the platform. Release points were counterbalanced such that for the four trials of a session, each release point (one from each wall, three in total) was used once, with the final release point being chosen randomly from the three options, with the stipulation that across three sessions each release point was used an equal number of times. The orientation of the arena was varied between trials, with each of the four possibilities (i.e., the apex of the arena pointing towards each cardinal compass point) used in each session, in a pseudorandom order. On session 19, the animals were given a single landmark test trial in the open circular pool, with both landmarks present, but with no platform present. For half of the animals, the prism landmark was in the north-east quadrant of the pool and the ball was in the south-west quadrant; this was reversed for the other half of the animals. Three of the five animals in each group experienced the correct landmark in the north-east quadrant of the pool, with the other two animals finding the correct landmark in the south-west. Animals were released from the center of the pool, equidistant from the two hanging landmarks, facing in a south-easterly direction. The time each animal spent searching for the platform underneath each landmark in circular zones, 50 cm in diameter and centered on each landmark, was recorded using EthoVision.

2.1.2 Results and Discussion

The time taken to locate the platform during training differed little between the two groups (Figure 2.2). A repeated measures Analysis of Variance (ANOVA) of Session x Landmark showed a significant main effect of session, $F(17, 136) = 50$, $p < .001$, with latencies to the hidden platform decreasing over the course of training. There was no main effect of landmark ($F < 1$). There was a significant interaction between session and landmark, $F(17, 136) = 2.0$, $p = .014$. Despite this interaction, on no sessions was there a significant difference in the time taken to find the hidden platform between animals trained with the ball correct and those trained with the prism correct, *F*s(1, 8) < 3.5, *p*s > .1.

Despite few differences between the two groups during training, Figure 2.3, which shows the results of the landmark test trial, reveals a greater preference

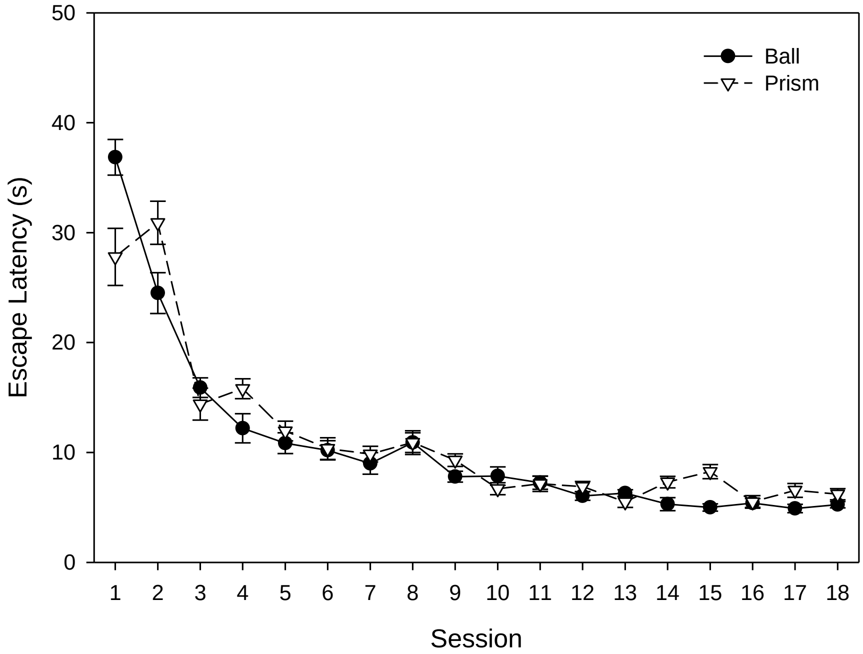


Figure 2.2: Escape latency data for the training stage, split by correct landmark. Error bars represent ± the Standard Error of the Mean.

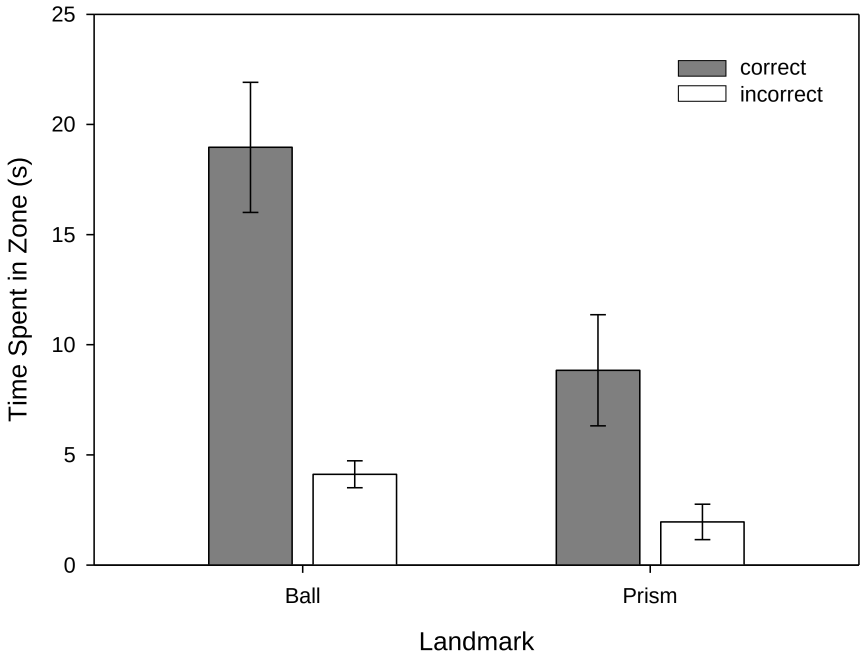


Figure 2.3: Time spent in the correct and incorrect zones in the landmark test trial, split by correct landmark during training. Error bars represent ± the Standard Error of the Mean.

for the landmark reinforced during training for Group Ball compared with Group Prism. A repeated measures ANOVA of Zone (landmark indicating the platform's presence during training, or the other landmark) x Landmark (ball or prism indicating the presence of the platform during training) confirmed this observation by revealing an interaction between these main effects, $F(1, 8) = 5.6$, $p = .046$. Analysis of simple main effects showed that both groups discriminated between the correct and incorrect zones, $Fs(1, 8) > 9.4$, $ps < .02$. However, Group Ball spent significantly more time in the correct zone than Group Prism, $F(1, 8) = 6.8$, $p = .03$. Groups Ball and Prism spent a similar amount of time underneath the incorrect landmark, $F(1, 8) = 4.6$, $p = .07$. There were also main effects of zone, $F(1, 8) = 42$, $p < .001$, and landmark, $F(1, 8) = 7.2$, $p = .028$, with more time spent in the correct zone than the incorrect zone, and more time spent exploring landmarks by Group Ball than by Group Prism.

The differences between the two groups in the landmark test suggest that those animals trained with the platform beneath the ball throughout training learned significantly more about the association between the ball and the platform than those trained with the prism learned about the association between the prism and the platform. This result reflects a difference in salience between the two cues, with more being learned about the more salient cue. It can be inferred from this that the ball landmark is relatively more salient than the prism landmark, when both are trained in compound with equivalent geometry cues. It is difficult to identify the reason for the difference in salience between the landmarks, although one possible reason is that the similarity between the features of the prism and those of the rest of the apparatus, such as the walls of the arena and the surrounding curtains, was greater than the similarity between the ball and the apparatus. As such, it is possible that the ball was a more intense stimulus than the prism.

Horne and Pearce (2011) found that a landmark of lower salience, when paired with geometry, should enhance geometry learning. If their findings also apply to a similar situation involving discrete landmarks, then it might be predicted that the prism used in Experiment 1 will be more likely to counteract overshadowing of geometry learning than the ball. Before considering the possible reasons for such an effect, Experiment 2 is presented, in which was tested the differential effect of the two discrete landmarks on geometry learning.

2.2 Experiment 2

Horne and Pearce (2011) attempted to examine the circumstances under which non-geometric panels attached to the walls of a rectangular arena potentiated or overshadowed geometry. They found that non-geometric cues of relatively low salience enhanced geometry learning, whereas those of high salience restricted the amount learned about geometry. Horne and Pearce (2011) appealed to their previous demonstration (Horne & Pearce, 2009b) of the presence of within-compound associations between the colors of the walls near the location of a submerged platform and the geometry of the arena to explain their potentiation results, although the nature of both the geometric and non-geometric cues differed between their studies.

In order to provide strong evidence for the role of within-compound associations in both failure to observe overshadowing, and potentiation, of geometry by non-geometric cues, it needs to be demonstrated that these cue competition effects and the presence of within-compound associations occur under the same circumstances. Therefore, Experiment 2 sought to examine how the differently salient landmarks from Experiment 1 would affect learning based on geometry. Given that a number of previous failures to demonstrate overshadowing of geometry have involved a triangular pool, these same geometric cues were used in Experiment 2. Rats were trained to locate a platform hidden in one of the two base corners of the arena. In addition, for half of the animals in the experimental condition the ball landmark indicated the platform’s position (with the prism over the other base corner) while the remainder received training with the prism indicating the platform’s position, with the ball over the other base corner. Two further groups were trained to act as a control against which the experimental groups’ performances could be compared. The platform was also hidden in one of the two base corners for these control groups, but the two landmarks over the base corners of the pool were identical. For half of the animals two balls were used, and for the remainder there were two prisms over the base corners (see Figure 2.4). During a test trial at the end of training, in which the landmarks and platform were removed for all of the animals, rats in these control groups were expected to have learned to rely on the geometry of the arena to locate the platform to a greater extent than those animals in the experimental groups, since the landmarks provided ambiguous information. The inclusion of these ambiguous landmark cues for the control groups allows us to control for generalisation decrement. In this regard, any differences between the control and experimental groups could not be explained by a greater difference between training and testing conditions for one group over the other, because landmarks were removed for all animals.

Standard models of associative learning would predict that the presence of the discriminable landmark cues for the experimental groups should restrict the amount learned about geometry. Therefore, the control groups, which can learn the position of the goal in reference only to the geometry, should demonstrate better geometry discrimination during the test trial, in which the non-geometric information is removed, than the experimental groups. However, given previous failures to observe overshadowing with similar geometric cues, and the demonstration by Horne and Pearce (2011) that the salience of the non-geometric cue alters the extent of overshadowing, it is difficult to make a prediction on the degree of cue competition that should be observed here. One thing that can be expected is that the lower salience landmark should overshadow geometry to a lesser extent than the higher salience landmark. In addition, the presence of within-compound associations may counteract any overshadowing effect observed.

2.2.1 Method

2.2.1.1 Subjects and Apparatus

Twenty experimentally naïve male Lister Hooded rats from the same stock as in Experiment 1 were used in this study. They were divided randomly into four equal groups at the beginning of the experiment. Other details were the same as for Experiment 1. The apparatus was the same as in Experiment 1 with the exception that animals in the control groups received training with two identical landmarks over the base corners of the triangular pool. Duplicates of the ball and prism landmarks from Experiment 1 were created for these groups.

2.2.1.2 Procedure

Animals were assigned randomly to one of four groups at the start of the experiment. Groups Ball-compound and Prism-compound received identical training to the Ball and Prism groups from Experiment 1. The other two groups of animals, Ball-control and Prism-control, were trained in a very similar manner, with the exception that instead of two discriminable landmarks they were presented with identical landmarks over each base corner, such that an accurate determination of the position of the hidden platform must be based on the shape of the arena alone. These control groups were not expected to differ in the extent to which they learned about the significance of the geometric cues for locating the platform, but their data are presented separately for clarity. Other details are as described for Experiment 1.

Following 18 sessions of training, all animals underwent a single geometry test trial. This took place in the same triangular arena as during training, with the apex facing south. There were no platforms or landmarks present during this test trial and, as during training, the curtains were drawn around the pool. Each animal was placed in the

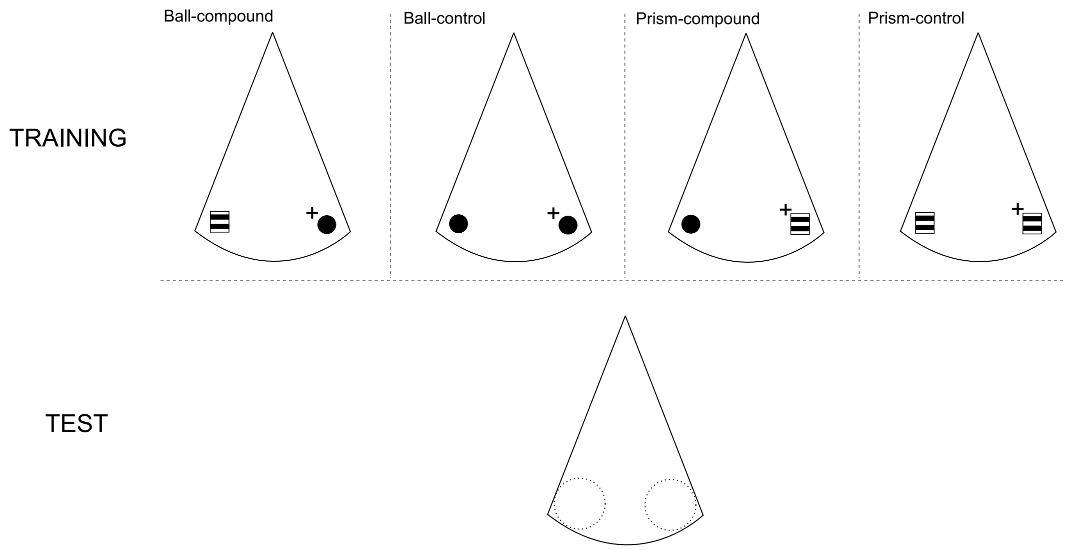


Figure 2.4: Standard overshadowing procedure used, in this case, to find potentiation of geometry learning by the presence of a distinct landmark cue, in Experiment 2. Filled black circles represent the ball landmark, horizontally striped rectangles represent the prism landmark, '+' signs denote the landmark under which the hidden escape platform is located, and the dotted areas denote the areas in which exploration times during the test trial are queried.

center of the water maze, facing south, and was allowed 60 s to search the arena. The animal was then removed from the north of the pool, dried, and returned to its carrying box. The time each animal spent searching for the platform in two 30 cm-diameter circular zones was recorded using EthoVision. These zones were located in the base corners of the triangle centered on the potential location of the platform during training.

2.2.2 Results and Discussion

Latency to find the escape platform was recorded for each training trial. The mean escape latencies for each session, split by condition and landmark, can be seen in Figure 2.5. A repeated measures ANOVA of Session x Condition (compound or control) x Landmark (ball or prism) showed a significant main effect of session,

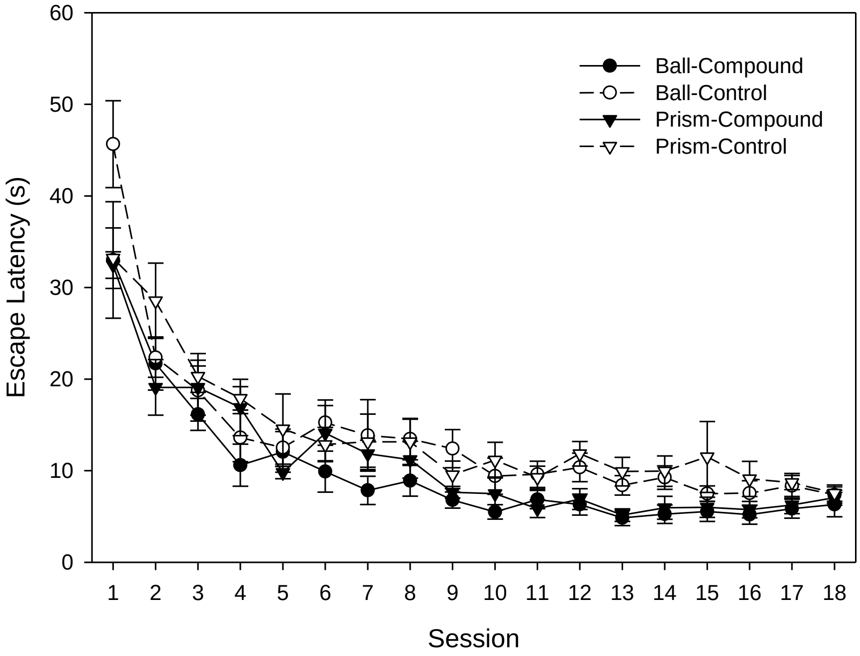


Figure 2.5: Escape latency data for the training stage, split by condition and landmark. Error bars represent ± the Standard Error of the Mean.

F(17, 272) = 68.70, *p* < .001, with a decrease in latencies over sessions. There was also a significant main effect of condition, *F*(1, 16) = 6.75, *p* = .019, with compound-trained animals showing significantly lower latencies than control animals. There was no main effect of landmark, or interaction between condition and landmark, *F*s(1, 16) < 1, and no interactions involving the session variable, *F*s(17, 272) < 1.7, *p*s > .05.

The results from the test trial in the triangle can be seen in Figure 2.6. While all groups spent more time in the zone in the base corner that had contained the platform during training than that which did not, this discrimination was strongest in the Prism-compound group. It can be seen that the Prism-compound group discriminated between correct and incorrect corners more than the Prism-control group. Although there was no potentiation of geometry learning for the Ball-compound group, neither was there evidence that the ball had overshadowed learning about geometry for this group, when

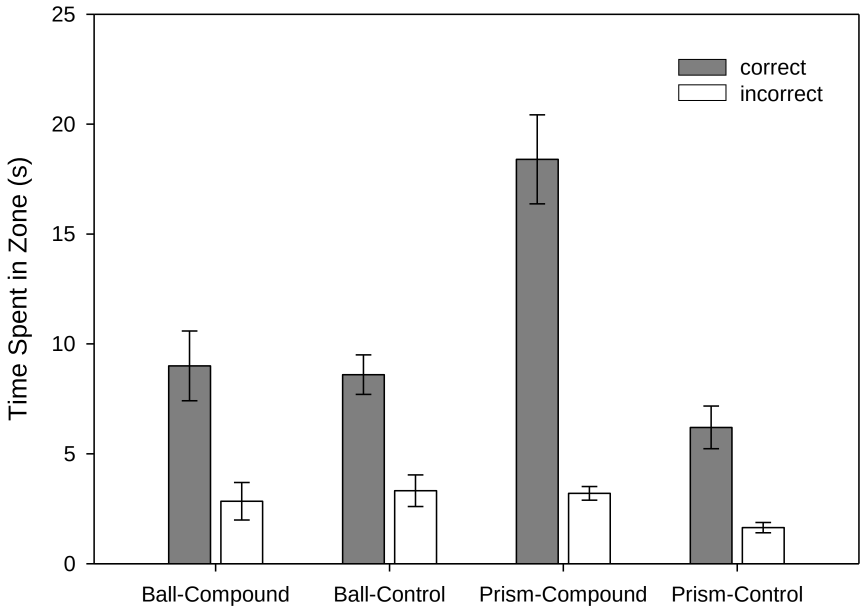


Figure 2.6: Time spent in the correct and incorrect corners in the geometry test trial, split by condition and correct landmark during training. Error bars represent ± the Standard Error of the Mean.

comparing its performance against that of the Ball-control group.

These observations were confirmed by the results of a repeated measures Condition x Landmark x Zone ANOVA which revealed a three-way interaction between these main effects, $F(1, 16) = 10.92$, $p = .004$. Further analysis of this interaction showed that when the prism was the correct landmark, there was an interaction between zone and condition, $F(1, 8) = 27.20$, $p = .001$, with the compound group spending more time in the correct zone than the control group, $F(1, 8) = 29.53$, $p = .001$. However, when the ball was the correct landmark, there was no interaction between zone and condition, $F(1, 8) < 1$, only a main effect of zone, $F(1, 8) = 28.70$, $p = .001$. The three-way ANOVA also showed significant main effects of zone and condition, and significant interactions between zone and condition, zone and landmark, and condition and landmark, Fs$(1, 16) > 7.90$, ps $< .02$. There was no main effect of landmark,

$F(1, 16) = 3.0$, $p = .10$.

The results are the first to show potentiation of geometry by a discrete landmark. They also demonstrate that this potentiation is only evident when the landmark is of relatively low salience. The results are in line with those of Horne and Pearce (2011), who also showed potentiation of geometry learning by their least salient landmark. It may have been expected that training geometry in compound with the higher salience ball landmark would result in overshadowing of geometry learning, based on Horne and Pearce’s (2011) similar design. However, their analysis of the causes of potentiation and overshadowing, as the result of within-compound associations counteracting different levels of overshadowing, provides a suitable explanation for such an apparent lack of overshadowing. Before accepting such an explanation, however, one other cause of the enhancement of geometry learning observed should be ruled out. Although these results are difficult to explain by appealing to traditional associative models, it may not have to be accepted that the superior performance of the Prism-compound animals was the result of potentiation as argued by Horne and Pearce (2011). From examination of the training results it is apparent that the compound-trained groups located the platform more rapidly than the control groups. If time taken to locate the platform is an indication of the extent to which learning has occurred then it may be argued that it is no surprise that compound-trained animals were superior in their discrimination of the correct and incorrect geometric corners of the pool in the geometry test. It should be noted, however, that although both Ball-compound and Prism-compound groups located the platform faster than the control groups, and as fast as each other, only the Prism-compound group showed any evidence that geometry learning was enhanced.

Therefore, the results of Experiment 2 are consistent with Horne and Pearce’s (2011) demonstration of the circumstances in which potentiation of geometry occurs, and also provide the first clear demonstration of potentiation of geometry learning by discrete landmarks. This same analysis can be applied to explain how within-compound associations between the more salient ball landmark and geometry were able to counteract any overshadowing of geometry. Although Horne and Pearce’s (2011) results are consistent with the within-compound association interpretation they provided, they did not measure the presence of the within-compound associations between their panel cues and the geometry of their arena. Accordingly, the purpose of Experiment 3 was to test for the presence of within-compound associations between the cues used in Experiments 1 and 2.

2.3 Experiment 3

In order to determine whether within-compound associations are a process by which potentiation and absence of overshadowing may occur in spatial learning, it is first necessary to demonstrate their presence using the same cues with which these effects are observed. Although within-compound associations have previously been shown in both an aversive water maze task (Horne & Pearce, 2009b) and an appetitive dry-maze task (Rhodes et al., 2009), their presence is unreported in a spatial task using the distinct compound of landmark and geometry cues that resulted in the potentiation observed in Experiment 2. It is important to note here that although within-compound associations have been implicated in the presence of potentiation, and absence of overshadowing, they have never been shown to exist between the cues most commonly used when observing these effects, that is spatially separate geometry and landmark cues.

Horne and Pearce (2009b) conducted an experiment that in part owed its design to a similar study by Durlach and Rescorla (1980), in which rats underwent flavor-odor aversion conditioning. Durlach and Rescorla observed that learning the relationship between the presentation of an odor and lithium chloride-induced illness was enhanced by the simultaneous presentation of a salient flavor, and supposed that this effect was the result of a within-compound association between the flavor and the odor. In the absence of the flavor rats learned little about the odor. To demonstrate the presence of the within-compound associations, following compound conditioning with the odor and flavor, they devalued one element of the compound, the flavor, by repeatedly presenting it in extinction. Subsequent testing with the odor alone demonstrated a reduced aversion to the odor when compared with a different odor that had also previously been paired with a flavor, but for which the flavor had not undergone extinction. Similarly, Horne and Pearce (2009b) showed that, following training in a kite-shaped arena with both the geometry of the arena and the colors of the walls indicating the location of the platform, revaluation of the wall colors altered the rats' response to the presentation of the geometric cues in the absence of the wall colors. In the same geometry test, a similarly trained group of rats that had not undergone revaluation of the wall colors, continued to demonstrate a preference for the corner of the kite that had contained the platform during training. The explanation for both Durlach and Rescorla's and Horne and Pearce's results was that in the final test, experiencing the cue with which the revalued cue was paired during compound training activated the memory for the revalued cue via the within-compound association. This memory failed to evoke a conditioned response, however, because the revaluation resulted in the extinction of response to the revalued cue. Any remaining response was the result of a direct association between the odor and illness in Durlach and Rescorla's case, and between the geometry and the platform in Horne and Pearce's.

The purpose of Experiment 3 was to determine whether the same revaluation effect could be observed on the rats' response to geometric cues, having previously experienced geometric cues in compound with landmark cues. Should the observations made in Experiment 2 be the result of within-compound associations between the geometry and landmark, then reducing the value of the landmark cue should reduce the rats' response to the corner of the pool associated with the platform during training, shown by a reduced discrimination between geometric cues. It was predicted that these within-compound associations would be shown to be present for all animals, regardless of the landmark beneath which the platform was located. Such a result would provide an explanation both for the potentiation of geometry by the prism seen in Experiment 2, and also for the lack of overshadowing of geometry by the ball in the same experiment.

The role of such associations in failure to observe overshadowing, and observation of potentiation, has been a matter of conjecture previously (Horne & Pearce, 2011; McGregor et al., 2009; Pearce et al., 2006) as the same cues have not been used to demonstrate both within-compound associations and these cue competition effects.

The experiment followed a similar design to that of Horne and Pearce (2009b). Following compound training in the same environment as used in Experiment 2, the prism-trained and ball-trained animals were each split into two equal groups such that the performances of each group were matched (see Figure 2.7). One of each of these prism- and ball-trained groups then underwent further training with the landmark, but in the absence of the geometric cues that were present during compound training. These groups were trained consistently with their previous training from stage 1: on trials in which the landmark that previously indicated the location of the platform was present,

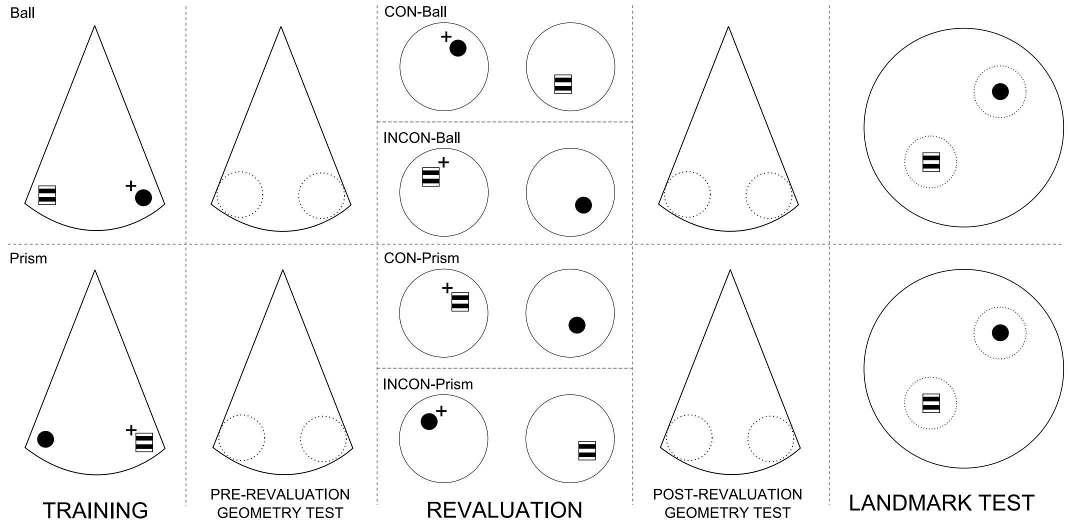


Figure 2.7: Procedure used for elucidating within-compound associations in Experiment 3. Filled black circles represent the ball landmark, horizontally striped squares represent the prism landmark, ‘+’ signs denote the landmark under which the hidden escape platform is located, and the dotted areas denote the areas in which exploration times during the test trials are queried.

the landmark continued to do so, while the previously unreinforced landmark was presented on other trials in the absence of the platform. The remaining animals were trained similarly, but with contingencies reversed: the previously reinforced landmark was presented on half the trials in extinction, while the previously unreinforced landmark was always presented with the platform beneath it, for the other half of the revaluation trials. For these inconsistently trained animals it was predicted that reversal training would result in a reduced discrimination between the base corners of the triangle when geometry alone was presented in a test trial at the end of the revaluation stage, compared with the consistently trained animals.

In addition, Experiment 3 allowed us to examine the properties of any within-compound association formed between landmarks and geometry. Should a less salient landmark form a much stronger within-compound association with geometry than a more salient landmark, the results of Experiment 2 need not be explained by appealing to within-compound associations counteracting differential overshadowing effects, as suggested by Horne and Pearce (2011). Instead, the stronger within-compound association could be assumed to allow a stronger representation of the non-geometric cue to be evoked from experience of the geometric cue. It is this stronger representation of the absent non-geometric cue that could result in potentiation of geometry learning. Should this be the case, then revaluation of the landmark following training to a compound of landmark and geometry cues should be more pronounced in the group trained with the landmark that produced greater potentiation. During the post-revaluation geometry test in the absence of the landmark cues, a stronger within-compound association should result in a more strongly evoked representation of the landmark cue. This representation should reduce the discrimination of geometry more than for the group that had formed a weaker within-compound association during compound training. As it has been demonstrated that the less salient prism landmark potentiates geometry more strongly than the more salient ball landmark, it would be expected that a stronger revaluation effect would be evident for the prism, if within-compound association strength accounts for the results of Experiment 2. Conversely, if the extent to which potentiation is observed is a result of differential overshadowing of geometry by landmark cues, then a similar revaluation effect, regardless of the identity of the correct landmark, would be expected.

2.3.1 Method

2.3.1.1 Subjects and Apparatus

Twenty experimentally naïve male Lister Hooded rats (*Rattus norvegicus*) were the subjects in this study, from the same stock as those used in Experiments 1 and 2. They were divided randomly in to two equal groups at the beginning of the experiment, and were later sub-divided in to two further groups based on their performance at the end of stage 1 of training. Other details were the same as for Experiments 1 and 2. The apparatus was the same as in Experiment 1.

2.3.1.2 Procedure

Animals were split into two groups based on the identity of the landmark under which the platform was located, and were trained in an identical fashion to those in Experiment 1 for the first 18 sessions, with the landmarks and the geometry of the arena in compound predicting the location of the platform. All animals then underwent a single geometry test trial, as described in Experiment 2, on session 19 in order to determine a baseline performance for geometry learning prior to the effects of any revaluation. Using this pre-revaluation geometry test (which showed the animals' preference for a particular corner based on which corner was previously reinforced) combined with the data from the 18 training sessions, the animals from each landmark group were sub-divided equally into two very closely matched groups, creating four groups in total, split by landmark (Ball or Prism) and whether animals received revaluation that was consistent or inconsistent with their training contingency (CON or INCON): CON-Ball, CON-Prism, INCON-Ball, and INCON-Prism.

Immediately following the geometry test trial, rats in each group received revaluation training relevant to the condition into which they had been placed. For all animals the landmarks were presented in the circular water maze with the curtains drawn around it. The landmarks were suspended from wires, painted white, which were attached to hooks on the circular ceiling above the pool. Groups CON-Ball and CON-Prism received, per session, two trials in which the platform was placed under the landmark that was reinforced during stage 1 training. In the remaining two trials the landmark that did not signal the platform’s location during stage 1 training was presented. In these trials, animals were required to swim in the pool for a duration of 60 s, in the presence of the landmark, but in the absence of the escape platform. Thus animals in the CON condition experienced direct reinforcement of the previously correct landmark, and direct extinction of the previously incorrect landmark. Groups INCON-Ball and INCON-Prism underwent similar revaluation treatment, but the reinforced landmark during stage 1 training was now presented in the absence of the platform, and the previously incorrect landmark was now presented with the platform beneath it. This treatment was intended to reverse stage 1 training regarding the location of the platform with respect to the identities of the landmarks. The revaluation stage lasted for five sessions, from session 20 to session 24. The rats were released from each of the four cardinal points of the pool once per session in a pre-determined random order. The landmarks could occupy any of twelve locations within the pool, chosen from 32 possible locations. The only stipulations on landmark position were that it should be no less than 28 cm from the center of the pool, no less than 40 cm from the edge of the pool, and not occupy the same quadrant of the pool for more than one trial per session.

Two test trials were presented following the conclusion of the revaluation stage, on sessions 25 and 26. The first was the critical post-revaluation geometry extinction test that was conducted in an identical fashion to the one conducted on session 19. Finally, a landmark test trial was presented, with both landmarks present but the platform absent. This test trial was conducted in an identical manner as the one described in Experiment 1 and was intended to provide a measure of the extent to which reversal learning had taken place during the revaluation stage for the INCON groups. A schematic diagram showing the order of the stages of the experiment is shown in Figure 2.7.

2.3.2 Results and Discussion

The time taken to find the hidden platform during stage 1 training was analysed using a repeated measures ANOVA of Session x Revaluation x Landmark. Animals were allocated to different conditions based on the results of the subsequent geometry extinction test, so it should be noted that to some extent the results are based on a post-hoc sub-division of animals, and as such, it was expected there would be no difference between revaluation conditions. The analysis showed a significant main effect of session, $F(17, 272) = 91.18$, $p < .001$, with latencies decreasing across sessions. There was no significant main effect of revaluation or landmark, and no interaction between these variables, $Fs(1, 16) < 1.55$, $ps > .2$. There were also no significant interactions

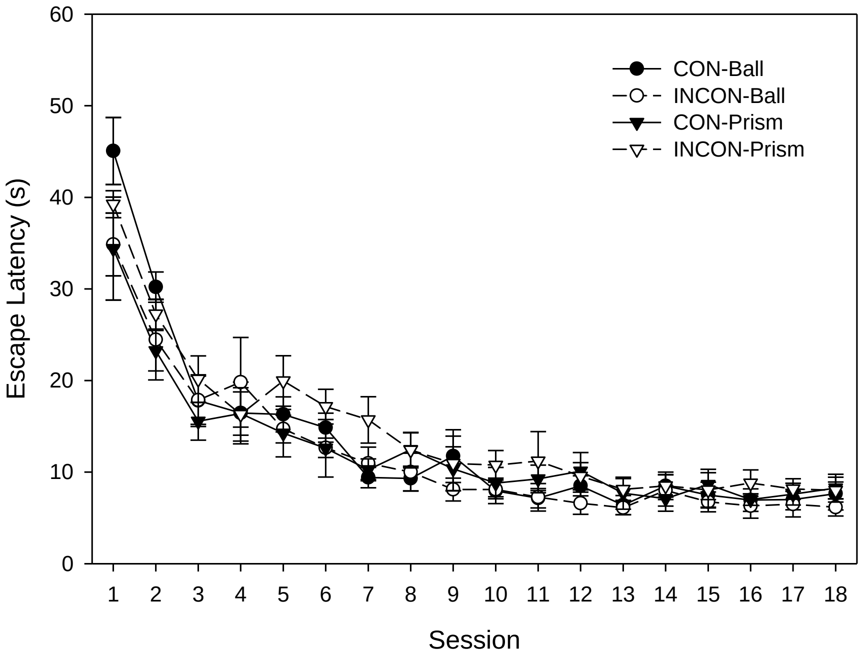


Figure 2.8: Escape latency data for stage 1 training, split by group and correct landmark. Error bars represent ± the Standard Error of the Mean.

involving the session variable, *F*s(17, 272) < 1.57, *p*s > .05. These results are shown in Figure 2.8, and imply that all groups, regardless of revaluation condition or correct landmark, showed both the same level and rate of learning about the location of the hidden platform when trained with a compound of geometry and landmark cues.

Mean times spent in the correct and incorrect base corner zones during the pre-revaluation geometry test are shown in Figure 2.9. A repeated measures ANOVA (Zone x Revaluation x Landmark) showed a significant main effect of zone, *F*(1, 16) = 18.17, *p* < .001, with more time spent in the correct zone than the incorrect zone. There was also a significant main effect of landmark, *F*(1, 16) = 6.43, *p* = .022, with more time being spent exploring the geometric cues by those animals trained with the prism landmark correct. This finding replicates Experiment 2, in which was observed potentiation of geometry learning by the presence of the prism landmark, but not when geometry was paired with the ball landmark. There were no other significant main effects, and no interactions between any other sets of variables, *F*s < 1.

For the revaluation stage, sessions consisted of both reinforced and non-reinforced trials. For the reinforced trials, learning about the landmark was measured using latency to find the platform (Figure 2.10). A repeated measures ANOVA (Session x Revaluation x Landmark) showed a significant main effect of session, *F*(4, 64) = 20.48, *p* < .001, with latencies to find the hidden platform showing a general decrease over sessions. There was also a significant main effect of revaluation, *F*(1, 16) = 7.27, *p* = .016, with those animals in group CON taking less time to find the hidden platform than those in group INCON. The interaction between session and revaluation variables approached significance, *F*(4, 64) = 2.33, *p* = .065, the simple main effects of which showed that animals in group CON found the platform

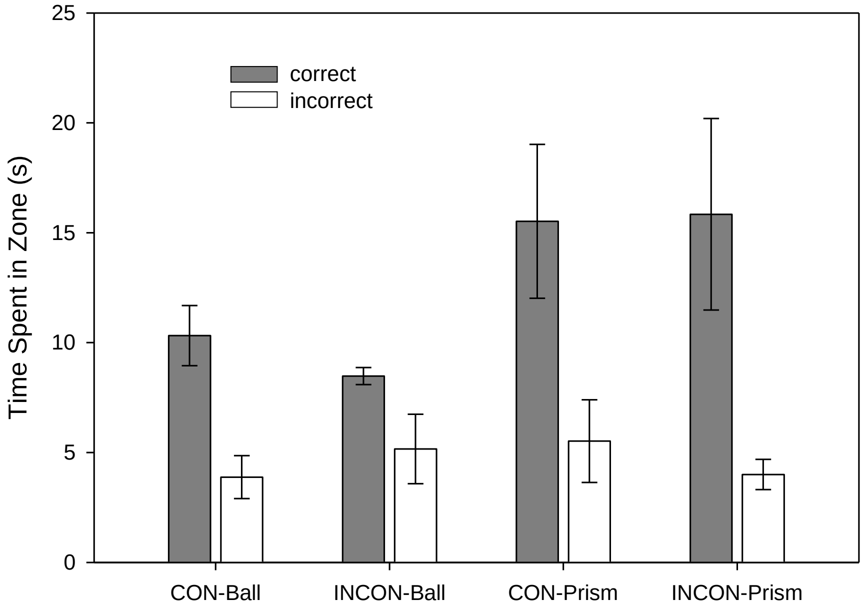


Figure 2.9: Geometry discrimination in the pre-revaluation geometry test, split by Revaluation and Landmark. Error bars represent ± the Standard Error of the Mean.

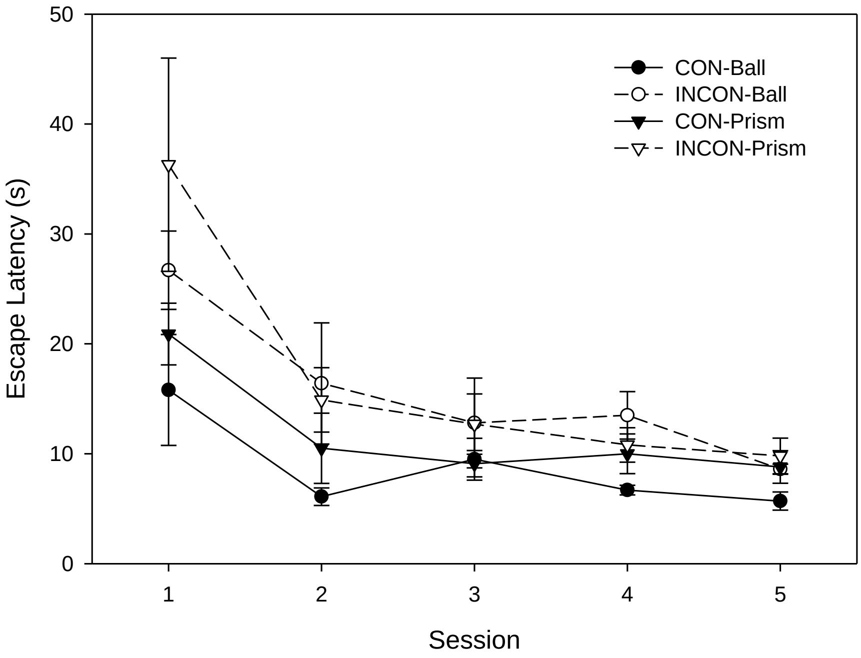


Figure 2.10: Escape latency data for the reinforced trials of the revaluation phase, split by condition and landmark. Error bars represent ± the Standard Error of the Mean.

significantly more quickly than those in INCON on session 1, *F*(1, 16) = 4.94, *p* = .041, session 4, *F*(1, 16) = 546, *p* = .033, and almost on session 2, *F*(1, 16) = 4.34, *p* = .054. There was no difference between conditions on either session 3 or 5, *F*s(1, 16) < 2.7, *p*s > .12. There was neither a main effect of landmark nor an interaction between landmark and revaluation, *F*s(1, 16) < 1. In addition, no other interactions involving the session variable approached significance, *F*s(4, 64) < 1.1, *p*s > .38.

In the crucial post-revaluation geometry test, the assignment of the correct and incorrect zones conformed to that of stage 1 of training (Figure 2.11). Importantly for the prediction of within-compound associations having formed between landmark and geometry cues during compound training, a repeated measures ANOVA of Zone x Revaluation x Landmark showed that there was a significant interaction between zone and revaluation, *F*(1, 16) = 6.51, *p* = .021. Analysis of the simple main effects of this

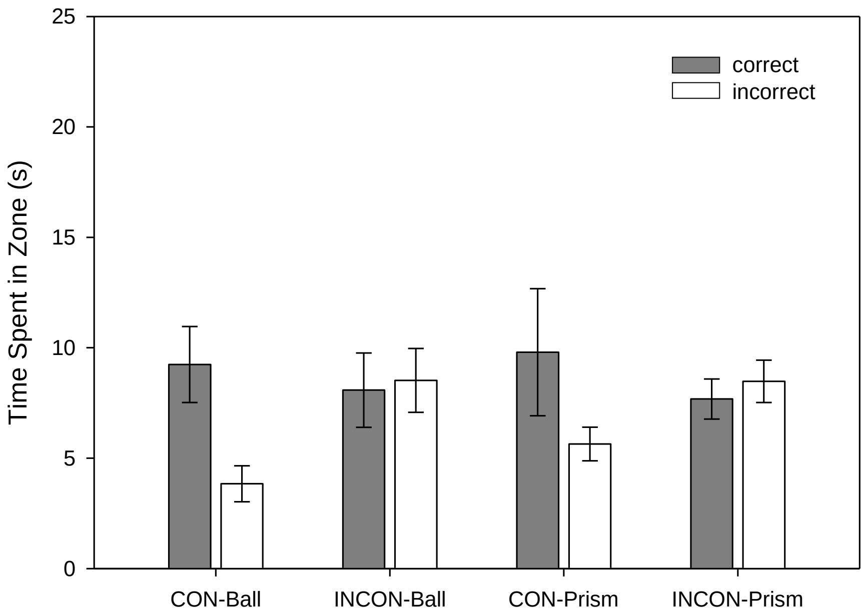


Figure 2.11: Geometry discrimination in the post-revaluation geometry test, split by Revaluation and Landmark. Error bars represent ± the Standard Error of the Mean.

interaction showed that group CON was able to discriminate between the correct and incorrect corners, *F*(1, 16) = 10.20, *p* = .006, whereas INCON lost their ability to perform this discrimination, *F* < 1, despite being similarly as competent as group CON at this discrimination in the pre-revaluation geometry test. Although there was no difference in the amount of time CON and INCON spent exploring in the correct zone, *F* < 1, INCON spent significantly more time in the incorrect zone than did CON, *F*(1, 16) = 13.30, *p* = .002. There were no other significant main effects or interactions from this analysis, *F*s(1, 16) < 3.86, including no three-way interaction involving the reinforced landmark during stage 1 training. This implies the effect of revaluation was similar between Ball- and Prism-trained groups.

In order to ensure that the landmark revaluation procedure had produced the required reversal of landmark preference for group INCON, and the effect was similar between groups INCON-Ball and INCON-Prism, the final landmark test trial recorded time spent searching for the platform underneath each of the two landmarks (see Figure 2.12). In addition, the test was intended to indicate that CON-trained animals retained the landmark discrimination they had learned during stage 1 training and had reinforced during the revaluation stage. A repeated measures ANOVA (Zone x Revaluation x Landmark) showed a significant Zone x Revaluation interaction, $F(1, 16) = 169$, $p < .001$. Analysis of simple main effects showed that whilst CON groups spent significantly more time searching for the hidden platform underneath the landmark that was correct during stage 1 training, $F(1, 16) = 127$, $p < .001$, INCON groups spent significantly more time searching underneath the landmark that was incorrect during stage 1 training, $F(1, 16) = 50.8$, $p < .001$. Additionally, CON groups spent significantly more time searching underneath the correct landmark than INCON groups, $F(1, 16) = 65.0$, $p < .001$, whereas INCON groups spent significantly more time in the proximity of the incorrect landmark than CON groups, $F(1, 16) = 93.7$, $p < .001$. The interpretation of this interaction is that the revaluation stage successfully reversed the landmark preference that INCON groups should have developed during initial training, with the preference now in favor of the landmark that was correct during the revaluation stage. Conversely, CON groups retained their preference for the landmark that was correct during initial training, as it remained correct during the revaluation sessions.

The inability of the INCON-trained groups to discriminate between the corners of the arena during the post-revaluation geometry test implies that their previous geometry preference had been abolished as a result of the landmark revaluation training, despite no difference between INCON- and CON-trained groups in their experience of which geometric cues were associated with the presence of the platform throughout training. The marked difference in the behaviors of the INCON and CON groups is

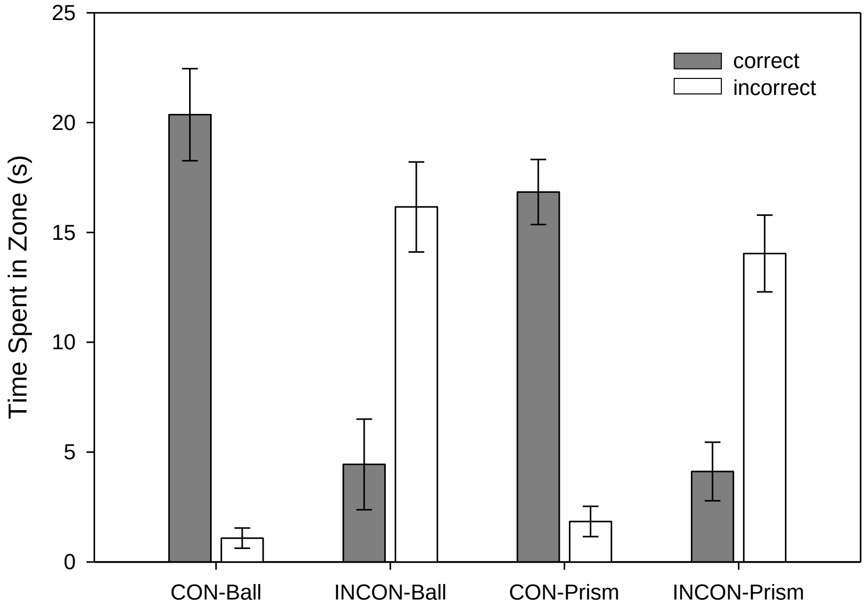


Figure 2.12: Landmark discrimination during the landmark test, split by group and landmark correct during training. Error bars represent ± the Standard Error of the Mean.

consistent with an account based on the formation of within-compound associations between the geometry and landmark cues during initial compound training. According to this account, in the post-revaluation geometry test the presentation of the corner that had contained the platform during training evoked a representation of the landmark with which it was paired in stage 1 training. For INCON-trained animals this evoked representation was not consistent with a representation for the presence of the platform, and thus the discrimination of geometric cues was poorer than that of the CON-trained animals, for which the evoked representation of the landmark was consistent with the platform's presence. The magnitude of the landmark revaluation appeared to be the same regardless of the identity of the landmark that had indicated the location of the platform during stage 1 training. This pattern of results is discussed further in the General Discussion.

2.4 General Discussion

In each experiment rats were trained to locate a submerged platform in one of the base corners of a triangular arena above each of which was suspended one of two distinctive landmarks. In Experiment 1 a landmark test in the absence of geometric cues established that the discrimination of the landmarks was more pronounced for those animals for which the platform was associated with the ball than with the prism. This finding led to the conclusion that the ball was a more salient landmark than the prism. In Experiment 2 rats trained to locate the platform beneath the prism in the same triangular pool subsequently showed superior geometry discrimination compared with rats in a control group for which landmarks provided ambiguous information about the location of the platform, and were therefore expected to learn the platform's location with reference only to the geometry of the arena. The presence of the ball above the platform for another group of animals appeared to have no effect on learning based on geometry. Experiment 3 tested the presence of within-compound associations under the same training conditions as Experiments 1 and 2 and suggested they had formed between both the ball and geometry and the prism and geometry. The results provide the first evidence, as far as I am aware, that the apparent immunity to cue competition between landmarks and geometry demonstrated elsewhere may in fact be the result of within-compound associations abrogating the overshadowing effect that is predicted by theories of associative learning. These results fail to support those theories that suppose learning based on discrete landmarks to progress independently of learning based on geometry (Cheng, 1986; Doeller & Burgess, 2008; Wang & Spelke, 2002, 2003).

This series of experiments is especially pertinent to the current spatial learning literature, as in the majority of studies that have failed to demonstrate an effect of non-geometric cues on learning based on geometry, the non-geometric cue was a discrete landmark, physically and visually separate from the walls that formed the arena’s shape (Hayward et al., 2003, 2004; McGregor et al., 2009; Pearce et al., 2001). Cheng (1986) and Gallistel (1990) proposed that learning based on geometry was impervious to learning based on any other non-geometric feature. However, some theories of spatial learning are more specific, postulating that it is only learning based on individual landmarks that fails to enter the same representation as geometric cues, and thus learning based on geometry progresses independently of these landmarks. For example, Wang and Spelke (2002, 2003) proposed that learning locations based on individual landmarks takes place egocentrically, while an allocentric representation of geometry is necessary only for reorientation. Similarly, Doeller and Burgess (2008) claim that a representation of location based on vectors derived from a uniform boundary is not influenced by a representation of location based on landmark position. Doeller et al. (2008) further suggest that boundary-learning and landmark-learning processes are independent of one another because the neural substrates for landmark- and boundary-learning are independent. In each of these cases, then, it is to be assumed that learning based on discrete landmarks will have no influence on learning based on geometry. Clearly, these theories have difficulty in explaining the recent work by Kosaki et al. (2013) that demonstrated overshadowing of geometry by discrete landmarks, and the work presented in the current study, in which the landmark and geometry cues must interact to form within-compound associations.

Although the results are not consistent with those theories that suppose spatial learning to hold a special status in learning and memory, other accounts assume no special role for learning based on geometry. For example, Miller and Shettleworth (2007) proposed a theory that was based on the Rescorla and Wagner (1972) error-correction theory with the addition of a probability rule to determine the likelihood of experiencing particular cue contingencies. Although their theory is able to explain the presence of potentiation between geometric and non-geometric cues within arenas with ambiguous geometric information, such as a rectangle, simulations of their model using the non-ambiguous geometric cues used in Experiment 1 produces only overshadowing. McGregor et al. (2009) presented simulations of Miller and Shettleworth’s model that also apply to Experiment 2, with an overshadowing group compared against a control group with two identical landmark cues paired with the geometry. These simulations showed that the associative strength of the correct geometry for the control group is always higher than that of the overshadowing group, thus the model predicts overshadowing of the geometric cue by the concurrently trained landmark cue. In addition, the account of cue competition put forward by Miller and Shettleworth cannot explicate the results of Experiment 3.

It has also been argued that template-matching can explain various aspects of spatial behavior within arenas of a distinctive shape (Cheung, Stürzl, Zeil, & Cheng, 2008; Stürzl, Cheung, Cheng, & Zeil, 2008). Template-matching theory would propose that an animal takes a snapshot of its surroundings while at the goal location. On future trials, the animal then moves around the arena in an attempt to match its current view with the stored view at the goal location. Minimizing the discrepancy between the current- and goal-views should lead the animal back to the goal location. However, all animals in Experiment 2 experienced a similar change in their environment between training and test conditions: all landmark cues were removed. It is unclear how this would cause poorer discrimination of geometry cues by the control group than by the compound group, and especially why this would depend upon the salience of the landmark above the platform in the manner observed. Additionally, there is no process within the template-matching account that could explain the change in discrimination between the base corners of the arena in Experiment 3 following revaluation of the landmarks. It is therefore unlikely that template-matching is able to explain any of the results presented in this chapter.

One objection to the interpretation of Experiment 1 regarding the salience of landmarks is that the within-compound associations formed between geometry and landmarks during compound training affected their discrimination during the test trial. Such an interpretation is perfectly valid, since it would not be expected that within-compound associations would affect the discrimination of geometry and not the discrimination of landmarks. However, the results of Experiment 3 show that the strength of the within-compound associations does not differ depending on the identity of the landmark. As such, while the presence of within-compound associations might have boosted discrimination for both Group Ball and Group Prism, the size of this effect should be similar for both groups. Any differences between the groups, therefore, can be ascribed only to differences in landmark salience.

The finding that reduction of the value of the landmarks in Experiment 3 affected geometry discrimination to the same extent regardless of the identity of the landmark suggests that the within-compound associations that formed between the ball and geometry, and the prism and geometry, were of a similar strength. It can be inferred from this that the mechanism by which within-compound associations affect cue competition is not based on differing strengths of the within-compound associations formed. Therefore, it is argued that the reason the less salient landmark potentiates learning about geometry, whereas the more salient landmark merely counteracts overshadowing, is due to differing degrees of overshadowing caused by these differently salient landmarks. Together with the results of Kosaki et al. (2013) and Horne and Pearce (2011), the results presented in this chapter provide an explanation for cue interaction effects observed between geometry and any non-geometric cue. The relative saliences of the cues determine both the degree of overshadowing, and the extent to which within-compound associations counteract overshadowing.

An explanation for the results of Experiment 3 in terms of within-compound associations having to overcome different degrees of overshadowing is consistent with accounts of within-compound associations in flavor-odor aversion conditioning, such as that offered by Durlach and Rescorla (1980). However, there is some discrepancy between the potentiation results in Experiment 2 and those of Durlach and Rescorla in terms of the relative saliences of the potentiating and potentiated cues. Whilst the prevailing experiments demonstrated potentiation of geometry cues by the least, but not the most, salient landmark, in flavor-odor aversion conditioning the opposite appears to be true. Durlach and Rescorla show potentiation of aversion learning of a low salience odor cue via compound conditioning with a relatively higher salience flavor cue. Despite this discrepancy, the observed potentiation is accounted for in a similar manner to ours, and that of Horne and Pearce (2011). These accounts suggest that testing in the presence of the non-revalued cues evokes representations of the revalued, but absent, cues, and it is these representations that affect discrimination of the non-revalued cues. This associative chain account supposes that when rats experience the correct geometric corner a memory for the absent landmark cue is evoked, and it is this landmark’s negative association with the escape platform that prevents animals from exploring this corner in preference to the incorrect corner. This account may be contrasted with one in which a configural representation of the landmark and geometry cues forms as a result of those cues being trained in compound. The revaluation of the landmark cue alone activates this configural representation, and the configuration of geometry and landmark cues is revalued. Experience of the geometry cues alone, during test, activates this configural representation, which has been revalued, resulting in animals failing to discriminate between correct and incorrect geometric cues (for a detailed discussion, see Dwyer, Burgess, & Honey, 2012). Currently the data from this chapter are unable to differentiate between these two mechanisms by which within-compound associations may have altered behavior towards geometric cues. It is possible that the apparent differences between conditions under which within-compound associations form in spatial and in non-spatial learning reflect the differences in these mechanisms. Understanding the mechanisms by which within-compound associations affect behavior is therefore an important step in determining whether the rules that govern spatial learning are unique.

CHAPTER THREE

Geometry Fails to Overshadow Landmarks

In Chapter 2 it was shown that within-compound associations formed between landmark and geometry cues when those cues were trained in compound. These within-compound associations enabled representations of absent cues to be evoked from the present cues with which they were paired during training, and those representations were able to influence behaviour towards the cues that were presented. The presence of these within-compound associations can explain both the absence of overshadowing (e.g., McGregor et al., 2009) and also the presence of potentiation (e.g., Pearce et al., 2006) of geometric cues by landmark cues in previous studies. Much of the focus of spatial cue competition has been on whether landmarks, discrete from (e.g., McGregor et al., 2009) or integrated with (e.g., Horne and Pearce, 2011) geometric cues, restrict learning based on those geometric cues. However, there have also been demonstrations of the reciprocal effect: the failure of geometric cues to overshadow learning about landmark cues. This failure has taken the form of potentiation of landmark cues by the presence of geometric cues, as well as an apparent lack of competition altogether. Horne and Pearce (2011) and McGregor et al. (2009) have both demonstrated that a group of animals trained to locate a hidden escape platform with reference to a compound of landmark and geometric cues learn more about the landmark cues in comparison to animals trained with only the landmark cues relevant for locating the platform throughout. It follows logically from Chapter 2 that these effects could also be explained by the already demonstrated presence of within-compound associations between landmark and geometry cues. However, the previous explanation of the mechanism by which within-compound associations can counteract cue competition effects relies on the evocation of representations of absent landmark cues via the presentation of geometry cues alone. In order for this explanation to hold true for those times when geometry fails to overshadow learning about landmark cues, it must also be demonstrated that the presentation of landmark cues alone can evoke representations of previously-paired geometry cues, and that these representations can influence animals' behaviour. Although Rhodes et al. (2009) have demonstrated reciprocal within-compound associations between geometric cues provided by a distinctive rectangular-shaped arena and the color of the arena's walls, this was in an appetitive sensory preconditioning paradigm, and not under conditions similar to those in which geometry cues have failed to overshadow landmark cues in the past. As in Chapter 2, a demonstration of the failure of geometric cues to overshadow landmark cues combined with the presence of within-compound associations between these same cues would constitute a strong argument that within-compound associations can account for the cue competition effects that have previously been observed.

Experiments 1A and 1B aimed to replicate the lack of overshadowing of landmark cues when trained in compound with geometric cues that has been shown previously (Horne & Pearce, 2011; Pearce et al., 2006). Experiment 2 attempted to demonstrate whether landmark cues were able to evoke a representation of concurrently trained geometry cues. Combined with the results of Chapter 2 Experiment 3, this would demonstrate reciprocal within-compound associations between landmark and geometry cues. In Chapter 2 it was shown that the salience of the landmark cues affected the extent to which the geometric cues were potentiated. Here, the same landmark cues were used and as such differential competition with geometric cues might be expected, as a consequence of the different saliences of the landmark cues. For this reason, and in an attempt to highlight any differences in overshadowing that a difference in the saliences of the landmarks may cause, it was decided to run two separate, but similar, overshadowing experiments. In Experiment 1A the position of the escape platform was predicted consistently by the presence of the less salient prism landmark, whereas in Experiment 1B the correct landmark was the more salient ball. It has been demonstrated previously that it is the less salient of these landmarks (the prism) that shows strongest potentiation of geometry learning. It has been argued that the reason for this is that the prism landmark overshadows the geometry less than the ball landmark, such that when the effects of within-compound associations are applied to both cases, the weak overshadowing caused by the prism landmark is more than compensated for, and potentiation is observed. However, the strong overshadowing caused by the ball landmark is only counteracted by the within-compound associations, but not reversed, resulting in neither overshadowing nor potentiation being observed. If the same logic is applied to the case of geometric cues overshadowing landmarks, it is conceivable that the prism landmark will be more overshadowed by the geometry than the ball landmark, owing to the lower salience of the prism landmark. Therefore, when the effects of within-compound associations are applied, it might be expected that the strong overshadowing afforded to the prism landmark is counteracted, whereas the weaker overshadowing of the ball landmark is reversed, and potentiation of the ball by the geometric cues is observed. These predictions are based on speculation that the saliences of landmark and geometric cues were not too dissimilar. If, on the other hand, the geometric cues were much less salient than the landmark cues, negligible overshadowing of the landmarks by the geometry might be expected, and as such applying the effects of within-compound associations should result in similar levels of potentiation of both landmark cues. Alternatively, the geometric cues may have been of much higher salience than the landmark cues, and strong overshadowing might be expected, regardless of the identity of the landmark cue. In such a situation, the effect of the within-compound associations may result in similar levels of compensation of overshadowing for both landmarks, but would perhaps be unlikely to show potentiation of landmark learning. These predictions all assume that the evoked representation of geometry should influence behaviour to the same degree as an evoked representation of landmark. It is possible that evocation of an absent geometry cue has either a much stronger, or a much weaker, effect on behaviour, in which case the predications above become less applicable to the results of this experiment. Regardless of the unknown relative saliences of the geometric and landmark cues, and any potential differential effects of their evocation on behaviour, the mechanism by which within-compound associations mediate the degree to which overshadowing of landmarks by geometry is observed still applies.

3.1 Experiment 1A

In order to apply the findings of Chapter 2 more broadly, and argue that the formation of within-compound associations between landmark and geometric cues can also account for the failure of geometry to overshadow learning about landmarks, this failure of overshadowing must be demonstrated using the same apparatus. In order to improve the chances of finding a difference in cue competition effects depending on the salience of the landmark cue that predicted the location of the escape platform, the number of animals trained with each landmark being correct was increased to ten, as opposed to the five animals per landmark that were used in the experiments of Chapter 2. For practical reasons, Experiment 1 was therefore split into 1A and 1B, such that for 1A all animals were trained with the prism landmark relevant, and for 1B the ball landmark indicated the location of the escape platform. Animals trained with a compound of landmark and geometry cues underwent exactly the same training as those used in the demonstration of potentiation, and lack of overshadowing, in Chapter 2. The ability of these animals to discriminate between correct and incorrect landmarks, in the absence of unambiguous geometry cues, was then compared with that of another group of animals, trained with only the landmark cues indicating the position of the escape platform throughout training.

3.1.1 Method

3.1.1.1 Subjects

The subjects were twenty male Lister Hooded rats (*Rattus norvegicus*) supplied by Harlan Olac (Bicester, Oxfordshire, England). They were between 200 and 250 g at the start of testing, and were not used in any other study before the experiment began. The animals were housed in pairs in cages in which they had continuous access to food and water. These cages were in a light-tight holding room on a 12 h light:dark cycle, with lights coming on at 8:00 am. The animals were always tested when the lights were on in their holding room, and at a similar time each day.

3.1.1.2 Apparatus

The apparatus for the training stage of this experiment was identical to that used in the experiments detailed in Chapter 2. The landmark test was conducted in a square-shaped arena, formed from four polyurethane boards. These boards were 114 cm long, 59 cm high and 0.5 cm thick and were suspended inside the pool on aluminium poles, in the same manner as those boards used to form the triangular-shaped arena. The square-shaped arena had a side-length of 114 cm and was centred such that the centre of the square coincided with the centre of the circular water maze. The landmarks were suspended over the surface of the pool in the same manner as for the triangular shaped pool: clear Perspex rods attached the landmarks to the poles suspending the polyurethane boards. These landmarks were suspended such that their centre was 25 cm from a corner of the square arena, on an imaginary line that bisected that corner. All other apparatus has been described in detail in previous experiments.

3.1.1.3 Procedure

The experimental design used in an attempt to observe cue competition was similar in concept to that used in Chapter 2 Experiment 2. One group of animals, group compound, was trained using a compound of landmark and geometry cues in exactly the same manner as in previous experiments. Another group of animals, group landmark, was trained under conditions in which only the landmark cues unambiguously indicated the position of the escape platform. For these animals, the geometry cues were unstable

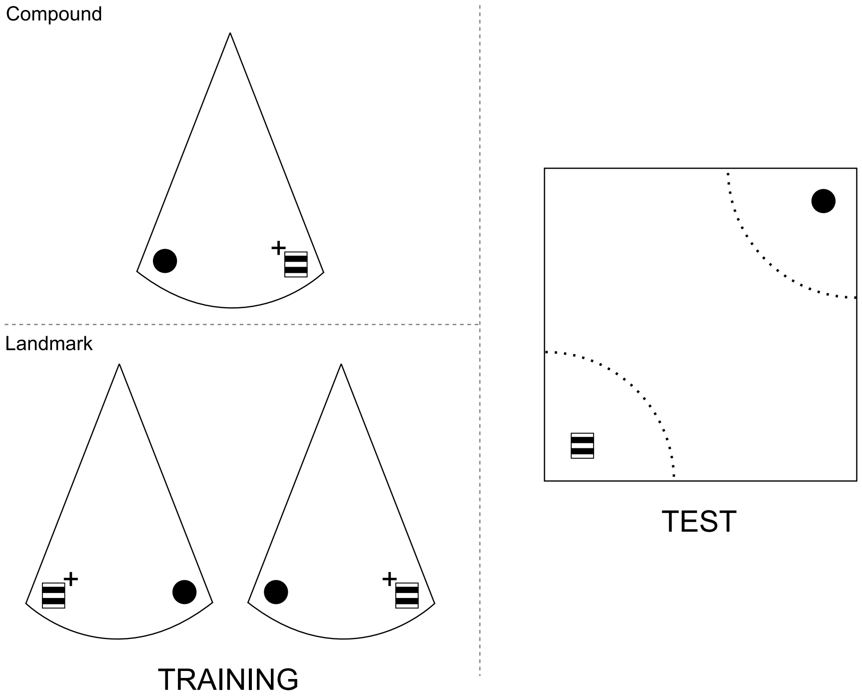


Figure 3.1: Schematic of the design used to determine whether geometric cues overshadow learning based on landmark cues. Plus (+) signs represent the presence of the escape platform. Dotted areas denote those places in which exploration times were queried to determine the extent of landmark learning.

with respect to the platform’s location. In Chapter 2 Experiment 2, it was possible to control for generalisation decrement between the control and compound groups by pairing both geometric cues with identical landmarks for the control groups. The analogous control for generalisation decrement in Experiment 1A would be pairing each landmark cue with identical geometric cues. In this manner, both groups of animals would experience the same generalisation decrement between training and test. However, due to the practical difficulties in presenting these identical geometric cues whilst retaining the same shape of the arena as that used for the compound group, it was necessary to give those animals in group landmark two different training contingencies (see Figure 3.1).

For half of the trials, the platform was underneath a particular landmark and located in one of the base corners of the triangular arena. The other landmark was located in the remaining base corner. For the rest of the trials, the platform was located underneath the same landmark, but both platform and landmark were located in the other base corner of the arena. The second landmark occupied the second base corner. In this manner, the landmarks remained a stable cue for the location of the hidden platform, but the geometric cues provided ambiguous information. Two measures of learning were recorded from these training trials: time taken to find the hidden platform, and proportion of trials in which the animal’s first choice of corner contained the platform. Imaginary arcs, of 30 cm radius, and centred on the intersections of the walls forming the corners of the triangular shaped arena, were used to determine which one of the three corners was visited first in each trial. After 18 sessions of training, of four trials per session (two trials with the platform and correct landmark in each base corner of the arena for those animals in group landmark), all animals were then placed into a square arena, in the absence of the hidden platform. This square arena provided only ambiguous geometric information, with all four corners being geometrically identical. One of the landmarks was suspended above each of the north-east and south-west corners of this square arena, the centres of which were 30 cm above the surface of the water maze. The identity of these landmarks was counterbalanced between groups, such that for each group the correct landmark was in the north-east corner for half of the animals, and in the south-west corner for the rest. The time that animals spent exploring in the proximity of these landmarks was used as a measure of the amount that had been learned about the relationship between each landmark and the location of the hidden platform. Proximity to these landmarks was defined by the head of the animal being within 45 cm of the intersection of the walls that formed the corner in which that particular landmark was located. Animals were released from the north-west corner of the pool facing into the corner and allowed to search for the absent platform for 60 s. All other procedural details are as described in Chapter 2 Experiment 2.

3.1.2 Results and Discussion

3.1.2.1 Training

3.1.2.1.1 Escape Latency

The times taken for animals to find the hidden platform during the training stage can be seen in Figure 3.2. It can be seen that both groups showed a decrease in latency to find the hidden platform across sessions. The two groups were closely matched for their times to find the platform, with perhaps those trained with only landmark cues relevant taking marginally longer than those trained with a compound of geometry and landmark cues.

This similarity in times taken for groups compound and landmark to find the platform was supported by the results of a mixed ANOVA (Group x Session) of mean individual latencies to locate the platform on each session. The following statistics have been adjusted using the Greenhouse-Geisser correction to account for a lack of sphericity in the session variable. A significant main effect of session, $F(5.1, 93) = 81.8$, $p < .001$, confirmed that animals showed a significant decrease in their times to find the platform across sessions. A non-significant main effect of group, $F(1, 18) = 2.50$, $p = .131$, indicated that both compound and landmark groups were similarly quick at finding the hidden platform. There was no interaction between session and group, $F(5.1, 93) = 1.17$, $p = .332$, suggesting that the rate of learning about the location of the platform was the same between groups.

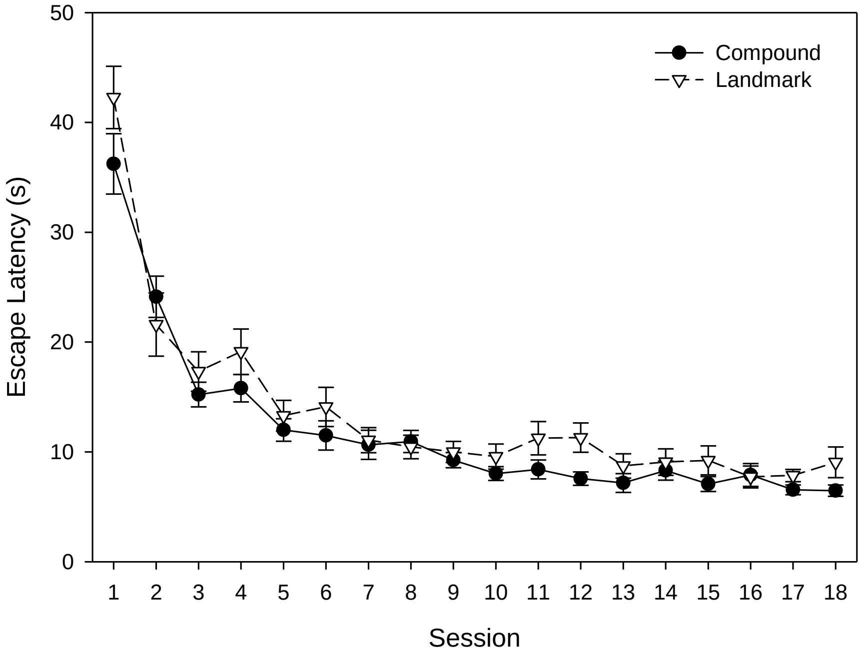


Figure 3.2: Escape latency for groups compound and landmark during training in Experiment 1A. Error bars represent ± Standard Error of the Mean.

3.1.2.1.2 First Choice

The proportion of initial visits to the correct corner for each session can be seen in Figure 3.3, with both groups showing similar improvements in their proportion of correct visits over sessions. Improvements in initial visits to the correct corner could imply learning about the location of the hidden escape platform.

A mixed ANOVA (Group x Session) of mean individual proportions of correct first choice on each session showed a significant main effect of session, $F(6.4, 116) = 9.54$, $p < .001$, indicating that the number of initial visits to the correct corner improved over sessions. There was neither a significant main effect of group, $F(1, 18) = .000$, $p = 1$, nor an interaction between session and group, $F(6.4, 116) = 1.55$, $p = .162$, suggesting that the performances of both groups were matched.

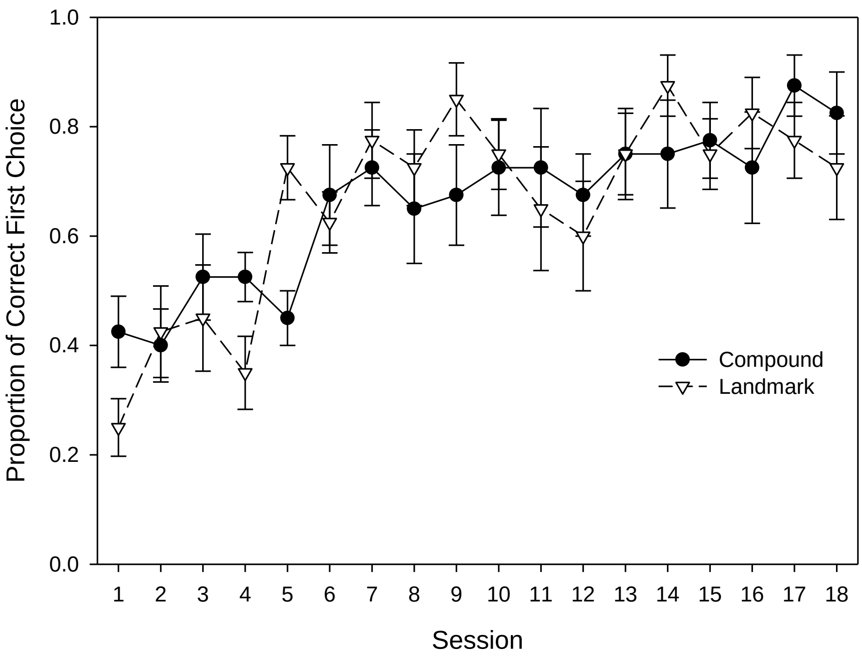


Figure 3.3: Proportion of first choices to the correct corner for groups compound and landmark during training in Experiment 1A. Error bars represent ± Standard Error of the Mean.

The analysis of training data showed that both measures of learning about the position of the hidden platform, latency to find the platform and initial search location, indicated an improvement in learning across sessions, with no differences between those animals trained with a compound of geometric and landmark cues, and those trained with relevant landmark, but ambiguous geometry, cues. These data speak to any differences between conditions in the landmark test being as a result of dissimilar landmark learning, rather than any differences in performance during training.

3.1.2.2 Landmark Test

The amount of time spent in two zones was recorded from the landmark test. One of these zones contained the correct landmark from training, and the other the incorrect landmark. The time that animals spent exploring within these zones can be

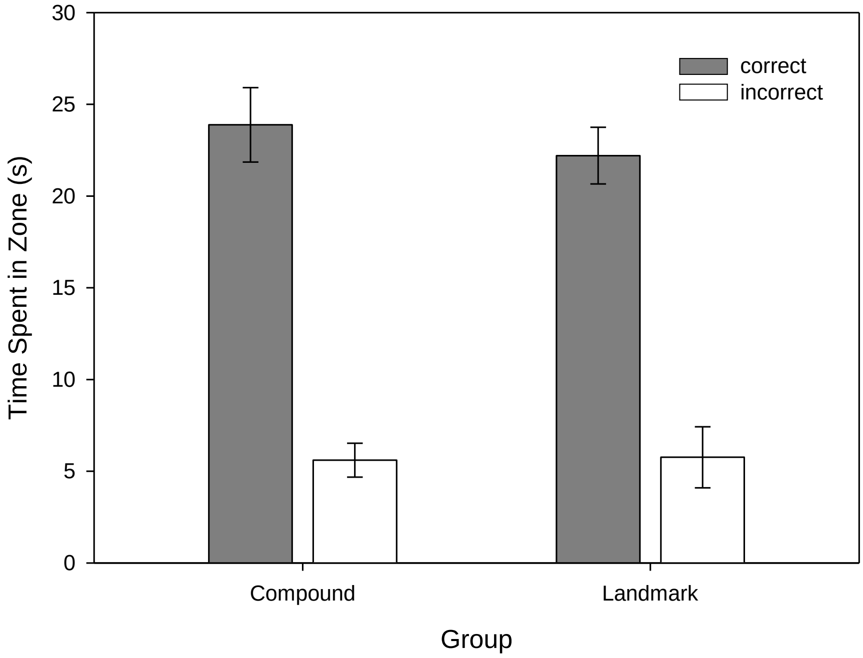


Figure 3.4: Time spent searching for the hidden escape platform underneath the correct and incorrect landmark cues in Experiment 1A. Error bars represent ± Standard Error of the Mean.

seen in Figure 3.4. Both groups spent a good deal more time searching for the hidden platform in the correct, rather than the incorrect, zone, and also appear to have discriminated between these zones to the same degree. A mixed ANOVA (Zone x Group) of time spent in the proximity of these two landmarks revealed a significant main effect of zone, $F(1, 18) = 70.8$, $p < .001$, with more time being spent in the zone containing the correct landmark than that containing the incorrect landmark. There was no main effect of group, $F < 1$, and no interaction between zone and group, $F < 1$.

This landmark test indicates that whether both landmark and geometry cues, or just landmark cues, were relevant for the location of the hidden platform, similar landmark learning occurred. This suggests a failure to show overshadowing of the landmark cues by the concurrent presence of reliable geometry cues. The results of McGregor et al. (2009), who found that their animals trained with a compound of cues learned significantly more about the relevance of landmark in locating the hidden platform than those trained with only landmarks as reliable cues, were not replicated by this experiment. However, their results were replicated in terms of a failure to observe the overshadowing of landmarks by geometric cues that most learning theories would predict. Before discussing the implications of such a finding, Experiment 1B is presented which replicated Experiment 1A with the alternative landmark.

3.2 Experiment 1B

Experiment 1A demonstrated that in rats trained to locate a hidden platform with a compound of the prism landmark cue and geometry, the geometric cue failed to overshadow learning about the position of the escape platform with reference to the prism landmark cue, when compared with an appropriate control. Experiment 1B followed closely that of 1A, except that in this case the landmark indicating the location of the escape platform was the more salient black ball.

3.2.1 Method

3.2.1.1 Subjects

The subjects were twenty male Lister Hooded rats (*Rattus norvegicus*) from the same stock as those used in Experiment 1A. They had not used in any other study before the experiment began. All housing and husbandry considerations were identical to those in Experiment 1A.

3.2.1.2 Apparatus

The apparatus used was identical to that in Experiment 1A.

3.2.1.3 Procedure

The procedure was very similar to that employed in Experiment 1A, with the only exception being that the landmark that indicated the position of the escape platform was the ball, as opposed to the prism in Experiment 1A.

3.2.2 Results and Discussion

3.2.2.1 Training

3.2.2.1.1 Escape Latency

Figure 3.5 shows the mean latency to find the hidden platform for animals in each group. As in Experiment 1A, escape latency decreased for both groups across sessions, and it appears that those animals in group landmark took marginally longer to find the hidden platform than those in group compound.

A mixed ANOVA (Group x Session) of mean individual latencies to locate the platform on each session showed a significant main effect of session, $F(5.1, 91) = 78.6$, $p < .001$, with the time taken to find the escape platform showing a general decrease across sessions. The main effect of group approached significance, $F(1, 18) = 4.2$,

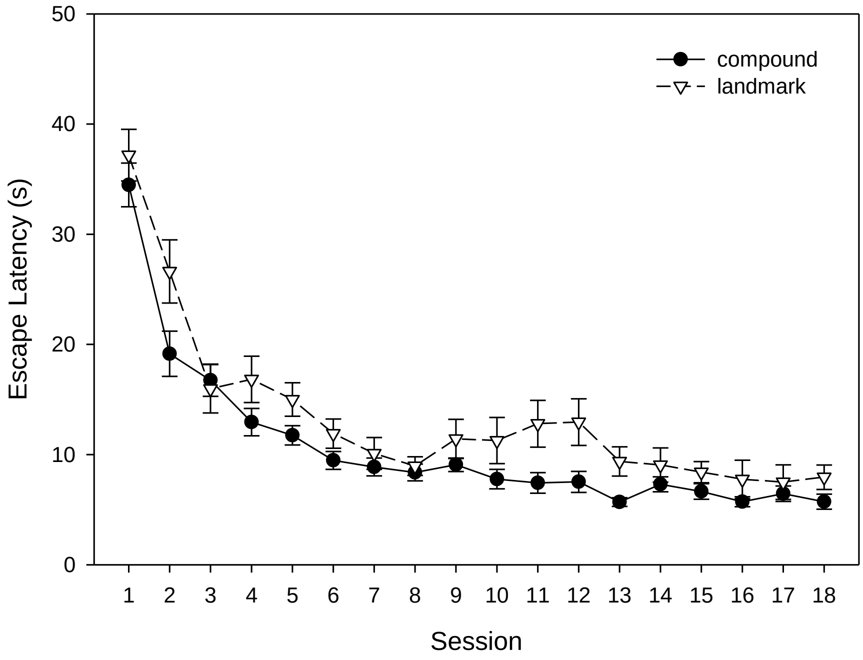


Figure 3.5: Time taken for groups compound and landmark to find the platform during training in Experiment 1B. Error bars represent ± Standard Error of the Mean.

p = .055, suggesting that those animals trained with a compound of landmark and geometry cues were quicker to find the platform than those trained with landmark cues alone. There was no significant interaction between session and group, *F*(5.1, 91) = 1.44, *p* = .218, indicating that the rate at which the two groups learned the location of the platform was similar.

3.2.2.1.2 First Choice

The proportion of initial visits to the correct corner for groups compound and landmark, during each session of training, can be seen in Figure 3.6. Both groups showed a general increase in their proportion of initial visits to the correct corner, with neither group showing better first choice performance than the other.

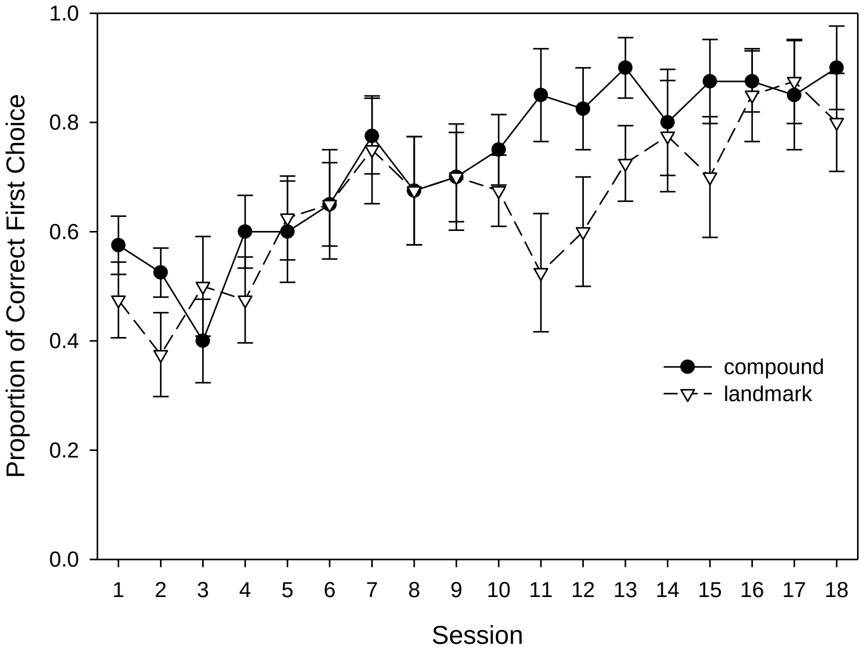


Figure 3.6: Proportion of first choices to the correct corner for groups compound and landmark during training in Experiment 1B. Error bars represent ± Standard Error of the Mean.

A mixed ANOVA (Group x Session) of mean individual proportion of correct first choice on each session showed a significant main effect of session, $F(6.5, 116) = 9.16$, $p < .001$, with the proportion of visits to the correct corner increasing over time. There was no significant main effect of group, $F(1, 18) = .881$, $p = .360$, and no interaction between session and group, $F(6.5, 116) = 1.45$, $p = .198$, suggesting that the proportion of initial visits to the correct corner, and the rate at which this measure improved over sessions, did not differ between those animals in the compound and landmark groups.

As in Experiment 1A, groups compound and landmark were matched on their first choice performance. However, in contrast to Experiment 1A, group compound appeared to take marginally less time to find the hidden escape platform than group landmark. As discussed in Chapter 2, this is not an inexplicable finding: those animals in group compound were able to learn the position of the hidden platform with respect to both geometry and landmark cues, as opposed to the landmark cues alone that provide positional information about the platform for the landmark group. In Experiment 1A, although there existed no significant difference between groups in the time taken to locate the hidden escape platform, those animals in group compound appeared to show lower latencies than those in group landmark. This is the same pattern of results as seen in this experiment, and again is explicable in that those animals in group compound were able to learn the location of the escape platform by reference to two cues.

3.2.2.2 Landmark Test

The time that each group of animals spent searching for the absent escape platform in the proximity of each of the landmarks during the landmark test can be seen

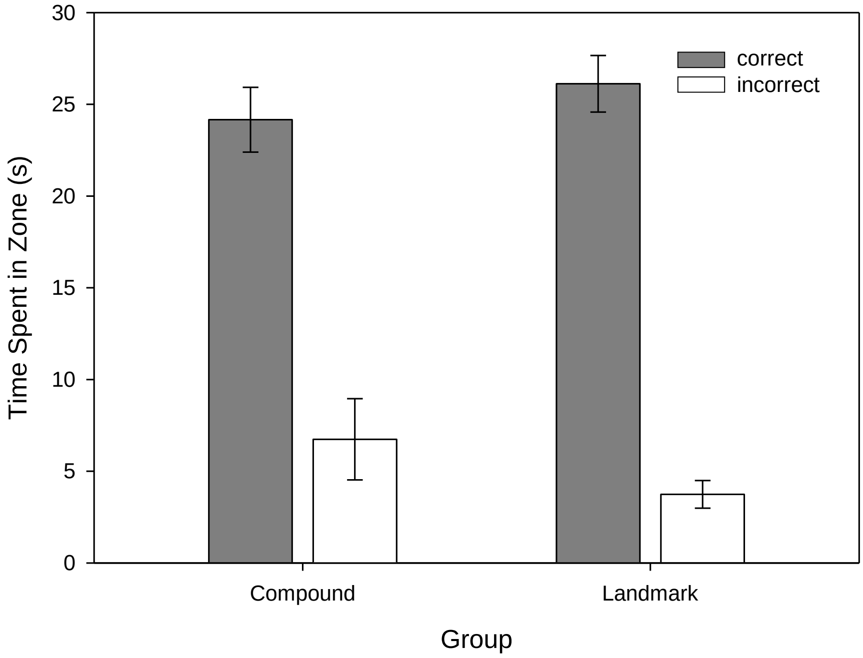


Figure 3.7: Time spent searching for the hidden escape platform underneath the correct and incorrect landmark cues in Experiment 1B. Error bars represent ± Standard Error of the Mean.

in Figure 3.7. These results can be seen to be comparable with those of Experiment 1A, with both groups spending more time searching for the hidden platform in the correct corner than the incorrect corner, and with little difference in the extent of this discrimination between groups.

A mixed ANOVA (Zone x Group) of the time spent near these landmarks showed a significant main effect of zone, $F(1, 18) = 103$, $p < .001$, with more time being spent searching near the landmark that had been correct, rather than incorrect, during training. The discrimination between correct and incorrect landmarks did not differ between groups compound and landmark, as indicated by the lack of a significant main effect of group, $F(1, 18) = .164$, $p = .691$, and importantly by the lack of an interaction between zone and group, $F(1, 18) = 1.60$, $p = .222$.

As in Experiment 1A, the landmark test here suggests that the presence of geometry cues for group compound did not restrict learning based on the landmark cues, when compared against group landmark, for which only landmark cues provided reliable information about the position of the escape platform. This, again, represents a failure of geometry cues to overshadow learning about the landmark cues. When taken with the results of Experiment 1A, these data suggest that geometry fails to overshadow landmark cues regardless of which of the differently salient landmarks the geometry cues should compete with. Despite not fully replicating McGregor et al. (2009) in showing potentiation of landmark learning by the presence of geometric cues trained in compound, a lack of overshadowing was observed. As discussed in Chapter 2, this failure to observe cue competition when geometric cues are present is of great interest to those attempting to determine whether traditional learning principles can be generalised to the spatial domain. Whether this lack of overshadowing was a result of similar learning about landmark cues between groups compound and landmark, or a consequence of the actions of within-compound associations has yet to be demonstrated. In Chapter 2, for both the failure to observe overshadowing of geometric cues by landmarks, and for the potentiation of geometry learning, an explanation in terms of within-compound associations was proposed. These within-compound associations, which have been shown to form between landmark and geometry cues from the work in Chapter 2, could also be the mechanism by which this failure of overshadowing of landmark cues by geometry manifests, following a similar argument to that discussed in detail previously. To demonstrate that those within-compound associations are reciprocal, that is they can be demonstrated via the revaluation of either landmark or geometry cues, would provide strong evidence that these associations are a mechanism by which lack of cue-competition between landmarks and geometry occurs, regardless of which cue fails to restrict learning based on the other.

3.3 Experiment 2

The previously demonstrated absence of overshadowing on geometry learning by a landmark has been shown to depend on the salience of the landmark cue, with the less salient of the two cues potentiating, rather than overshadowing, geometry learning. It was also shown in Experiment 3 of Chapter 2 that changing the animals' behaviour towards the landmark cues, through their revaluation, can indirectly alter behaviour towards the geometry cues with which the landmark cues had been trained in compound. This demonstrated that within-compound associations formed between landmark and geometry cues, and experience of geometry cues alone could evoke a representation of the landmark cues, which could affect performance towards the geometry cues. In Experiments 1A and 1B in this chapter, it was shown that the presence of geometry cues did not result in the overshadowing of landmark cues when these two types of cue were trained in compound. Although it has been previously shown that within-compound associations formed between landmark and geometry cues, and also that experience of the geometric cues evoked representations of the absent landmark cues, it does not necessarily follow that experience of landmark cues allows representations of the geometric cues to be evoked. This is an important distinction as, in Experiments 1A and 1B above, the animals were tested in the presence of landmark cues alone, in the absence of unambiguous geometric information. Therefore, in order for within-compound associations to have counteracted any overshadowing effects, representations of the absent geometric cues needed to have been evoked from the landmark cues. The work of Chapter 2 does not necessarily imply that these representations were evoked, and so the presence of within-compound associations between landmark and geometry cues needs to be shown again, but this time with the revaluation of the geometry cues. The effect of this revaluation on the animals’ behaviour towards landmark cues must then be tested, in a reversal of Chapter 2 Experiment 3.

This test of the presence of within-compound associations followed a very similar design to that of Chapter 2 Experiment 3, except that the revaluation stage involved revaluation of the geometry, rather than the landmark cues, and the effect of this revaluation was tested by observing animals’ landmark preference, rather than the geometry preference that was tested previously (see Figure 3.8). During training, the landmark and geometry cues that indicated the location of the platform were counterbalanced. No differences were expected based on the identity of the landmarks or geometry cues given the results of Experiments 1A and 1B. The revaluation stage involved the presentation of both geometric cues in every trial: for group CON the platform remained in the same corner of the triangular arena as during compound training, but for group INCON it was moved to the other base corner. This is in contrast to the revaluation stage of Chapter 2 Experiment 3, in which only a single cue was presented in each revaluation trial. On half of these trials, one landmark was experienced with the platform present, and on the rest the other landmark was present in the absence of the escape platform. A revaluation stage of interleaved reinforcement and extinction trials such as this was not possible with the revaluation of geometry cues as there are many practical difficulties inherent in presenting only a single geometric cue that is formed from an arena’s shape. However, demonstrating a difference in post-revaluation performance between groups CON and INCON using a different revaluation procedure than used previously can only help to strengthen the argument that within-compound associations exist between the landmark and geometry cues trained in compound. The landmark tests in this experiment were conducted in a circular arena, as opposed to the square arena used in Experiments 1A and 1B. It was felt that the square

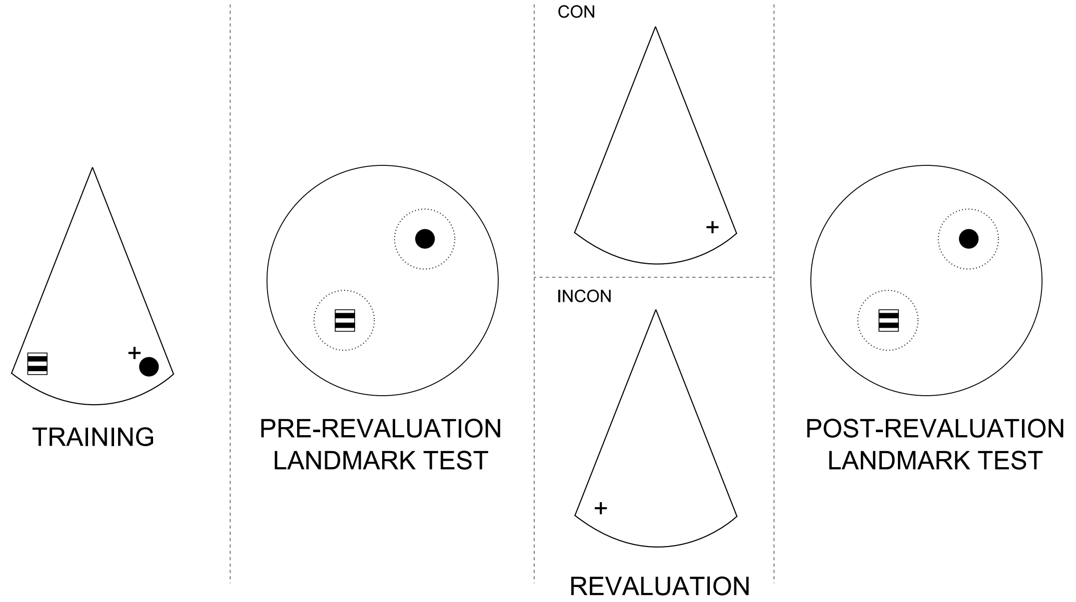


Figure 3.8: Schematic of the design for Experiment 2. Plus (+) signs represent the position of the hidden escape platform. Dotted areas denote those places in which exploration times were queried to determine the extent of landmark learning.

arena provided geometric information, albeit ambiguous, too similar to that experienced during training. In an effort to reduce the chance of this geometric information interfering with the evoked representation of geometry expected as a consequence of experiencing the landmark cues, as little geometric information as possible was provided by the arena.

In addition to the groups used in the previous demonstration of within-compound associations, it was decided to include an additional group of animals. This group (group NON) underwent the exact same training as the other two groups, but was exempt from the revaluation stage. It has been shown that the presentation of a single element of a previously trained compound of cues weakens the within-compound association between those cues (e.g., Rescorla & Freberg, 1978). Therefore, the revaluation training could have weakened the within-compound associations, the presence of which this experiment was attempting to demonstrate. By including a group of animals for which this weakening of the within-compound associations should not have occurred, the magnitude of this effect could be observed. Should the presence of within-compound associations not be demonstrated in this experiment, this may be due to their weakening through revaluation training, rather than evidence of their absence. It was argued, in Chapter 2, that the formation of within-compound associations between landmark and geometry cues is the mechanism by which potentiation, and lack of overshadowing, of geometry learning via concurrent training with landmarks occurred. As it was demonstrated in Experiments 1A and 1B that the presence of geometry failed to overshadowing learning about landmark cues, the obvious prediction was that evidence of within-compound associations should also be seen in this experiment. If no within-compound associations were apparent, and no weakening of the within-compound associations as a consequence of revaluation training was observed, then within-compound associations as a mechanism for potentiation, and the failure to show overshadowing, would be called into question.

3.3.1 Method

3.3.1.1 Subjects

The subjects were thirty male Lister Hooded rats (*Rattus norvegicus*) supplied by Harlan Olac (Bicester, Oxfordshire, England). Animals were between 200 and 250 g at the start of testing, and had not been used for any other study before the experiment began. All housing and husbandry considerations were identical to those in Experiment 1A.

3.3.1.2 Apparatus

All apparatus used in this experiment has been described in detail previously.

3.3.1.3 Procedure

A schematic of the procedure used in this experiment can be seen in Figure 3.8. All groups of animals initially underwent the same 18 sessions of training in the triangular-shaped arena. This comprised training with a compound of landmark and geometry cues present, and was identical to the training received in Chapter 2 Experiment 2 by group compound. All animals were then given a test to determine the extent to which landmark cues gained control of their behaviour. This test proceeded in the same manner as the landmark test of Chapter 2 Experiment 2, with one exception. The diameter of the circular zone surrounding each landmark, time in which constituted searching near that landmark, was reduced in diameter from 30 cm, to 16 cm. With an increase in the number of revaluation sessions between pre- and post-training revaluation geometry tests, it was feared that landmark discrimination would suffer, as a result of not having been trained with landmarks for some time. The smaller search zone was thought necessary to increase the sensitivity of detecting discrimination between these landmark cues, by reducing the noise generated by random swimming. This pre-revaluation landmark test was then followed by a revaluation stage. This was the first stage in which the training experienced by the groups of animals differed. Animals were divided into three similar groups, such that all groups were matched on performance during training and the pre-revaluation landmark test. Group NON had no training during this stage, and remained in their home cages until the post-revaluation landmark test. Groups CON and INCON were given eight sessions of training, of four trials per session, in the absence of landmark cues, but in the familiar triangular-shaped arena.

Group CON could find the escape platform in the same corner in which it was located during initial training. For group INCON, the location of the escape platform was moved to the previously incorrect base corner of the triangular arena. Following the same protocol as during initial training, animals were released from each of the three walls of the arena and the arena was rotated between trials. After this revaluation training, all three groups were then given the post-revaluation landmark test, conducted in exactly the same manner as the pre-revaluation landmark test.

3.3.2 Results and Discussion

3.3.2.1 Training

3.3.2.1.1 Escape Latency

The times taken for groups CON, INCON, and NON to find the hidden escape platform during training with a compound of landmark and geometry cues can be seen in Figure 3.9. All three groups showed a decrease in the time taken to find the hidden platform across sessions, and, as all groups of animals were trained identically during this stage, it is no surprise that all three groups took a similar amount of time to find the escape platform.

A mixed ANOVA (Group x Session) of mean individual times to locate the platform on each session indicated a significant main effect of session, $F(4.5, 121) = 142$, $p < .001$, with the time taken to find the escape platform generally decreasing over time. This decrease in latencies was similar for all three groups, with no significant main effect of group, $F(2, 27) = .145$, $p = .866$, and no interaction between session and group, $F(8.9, 121) = 1.45$, $p = .175$.

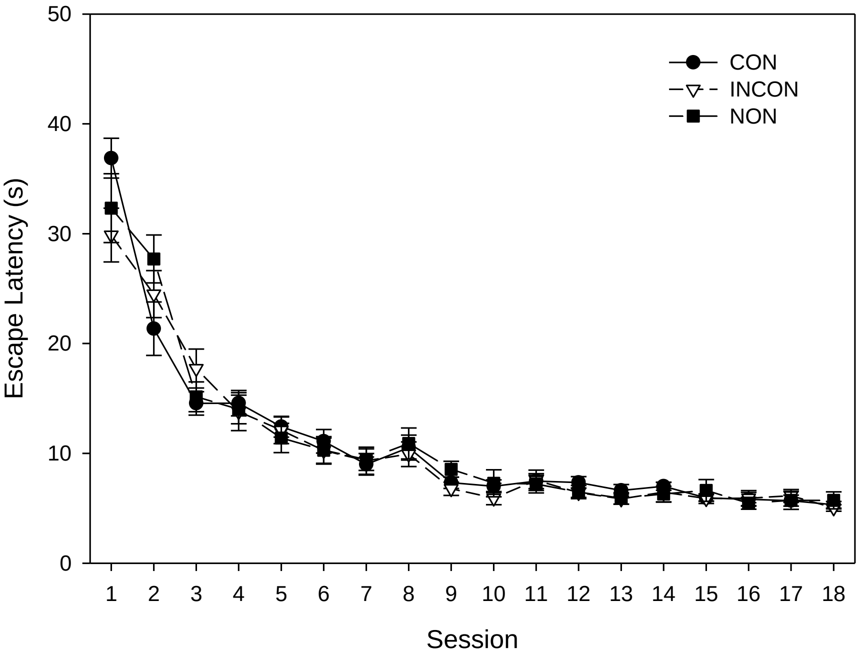


Figure 3.9: Time taken for groups CON, INCON, and NON to find the platform during training in Experiment 2. Error bars represent ± Standard Error of the Mean.

3.3.2.1.2 First Choice

The proportion of first visits to the correct corner during training for groups CON, INCON, and NON are shown in Figure 3.10. The proportion of initial visits to the correct corner increased across sessions for all groups, with little difference between the identically trained groups.

A mixed ANOVA (Session x Group) of mean individual proportion of correct first choice on each session showed a significant main effect of session, *F*(6.7, 180) = 29.8, $p < .001$, with the proportion of correct visits showing an overall increase over time. This increase in correct first choice was similar between the three groups, with there being no significant main effect of group, *F*(2, 27) = .101, $p = .904$, and no interaction between group and session, *F*(13.4, 180) = .507, $p = .921$.

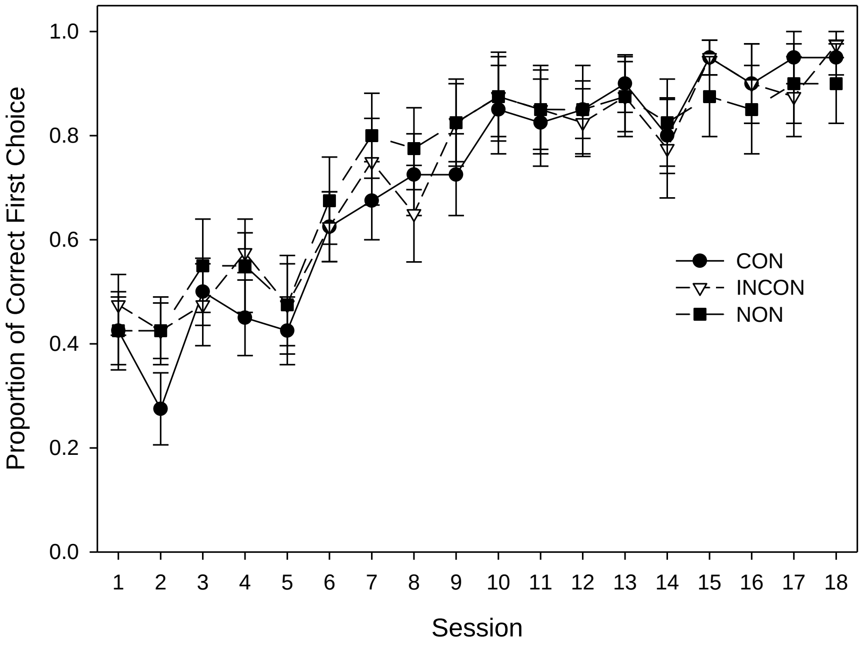


Figure 3.10: Proportion of first choices to the correct corner for groups CON, INCON, and NON during training in Experiment 2. Error bars represent ± Standard Error of the Mean.

Analysis both of the time taken to find the hidden platform and of proportion of correct first choices suggested that there were no differences between the three groups of animals either during, or at the end of, training. This is not surprising as all animals underwent the exact same training, but is necessary for any differences observed during the later manipulations to be attributed to these manipulations rather than to differences in performance during training.

3.3.2.2 Pre-Revaluation Landmark Test

Although the time taken to find the platform data and the proportion of correct first choice data indicate that animals in all three conditions performed similarly throughout training, a measure of the amount they had each learned about the landmark cues at the conclusion of this compound training is necessary. If differences in landmark performance are to be argued to be based on different revaluation procedures, similar landmark performance between the groups first needs to be demonstrated before those differences in procedure were applied. The escape latency and first choice performance during compound training do not necessarily indicate equivalent landmark learning, given that animals can learn the location of the escape platform by reference to either landmark or geometry cues. Figure 3.11 shows the amount of time each group of animals spent exploring near the landmark that indicated the location of the escape platform during compound training, compared with time spent exploring underneath the incorrect landmark. All three groups showed a similar discrimination between these landmarks, with all groups spending more time searching for the platform near the correct, rather than the incorrect, landmark. It should be noted that although the exploration times appear to be very low compared with those of Experiments 1A and

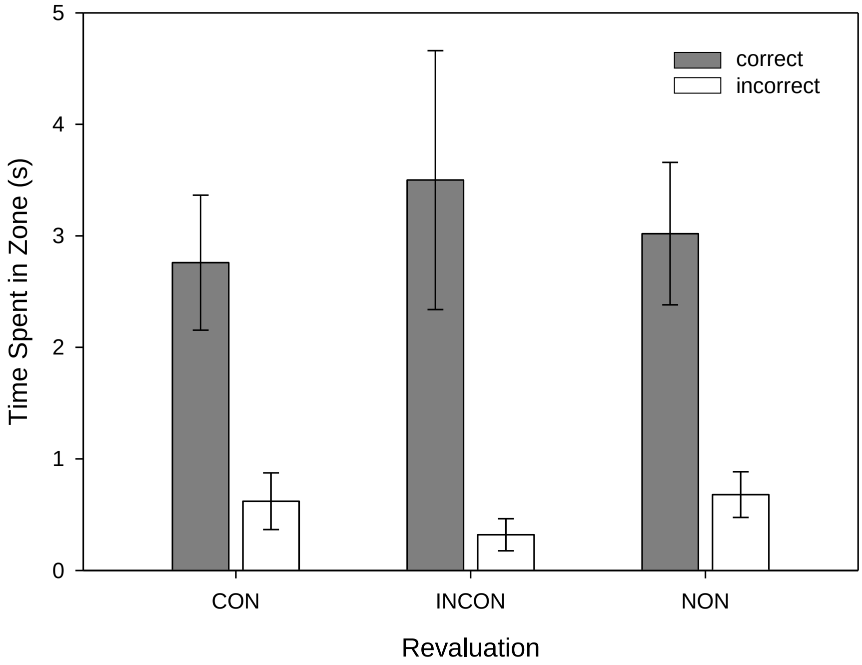


Figure 3.11: Time spent searching for the hidden platform underneath the landmark cues during the pre-revaluation landmark test in Experiment 2. Error bars represent ± Standard Error of the Mean.

1B, they are comparable when taken relative to the size of the zone in which exploration was measured. The zone areas in Experiment 2 were nearly eight times smaller than in Experiments 1A and 1B, in order to increase the sensitivity of the task. Accordingly, the exploration times are approximately eight times smaller.

A mixed ANOVA (Zone x Group) of time spent in the proximity of the landmarks showed a significant main effect of zone, $F(1, 27) = 33.6$, $p < .001$, with more time being spent exploring underneath the correct landmark than the incorrect landmark. Animals in all three conditions discriminated between correct and incorrect landmarks to a similar degree, with no significant main effect of group, $F(2, 27) = .056$, $p = .945$, and no interaction between zone and group, $F(2, 27) = .524$, $p = .598$. It can be inferred from these data that all three groups learned a similar amount about the relationship between the correct landmark and the location of the hidden escape platform.

3.3.2.3 Revaluation

During the revaluation stage of this experiment, only groups CON and INCON were subjected to training within the water maze. Group NON experienced no training during this period. As such, data and statistics for this stage include only groups CON and INCON.

3.3.2.3.1 Escape Latency

The time taken to find the hidden escape platform, which was present during all revaluation trials, for groups CON and INCON is shown in Figure 3.12. Unsurprisingly, group CON were able to find the platform more quickly than group INCON initially, as group CON were required to search in the corner in which the platform was always located. Conversely, for group INCON, the platform was located in the corner that did not contain the platform during training. Towards the end of the revaluation stage, group CON remained quicker than group INCON at finding the platform, but this difference in performance was less pronounced than at the start of the revaluation stage.

A mixed ANOVA (Session x Revaluation) of time taken to find the escape platform showed a significant main effect of session, $F(4.6, 82) = 9.25$, $p < .001$, with time taken to find the platform showing a general decrease over sessions. There was also a significant main effect of revaluation, $F(1, 18) = 26.2$, $p < .001$, with those animals in group CON having a consistently lower latency to find the platform than those in group INCON. The interaction between session and revaluation approached significance, $F(4.6, 82) = 2.35$, $p = .053$. Analysis of the simple main effects of this

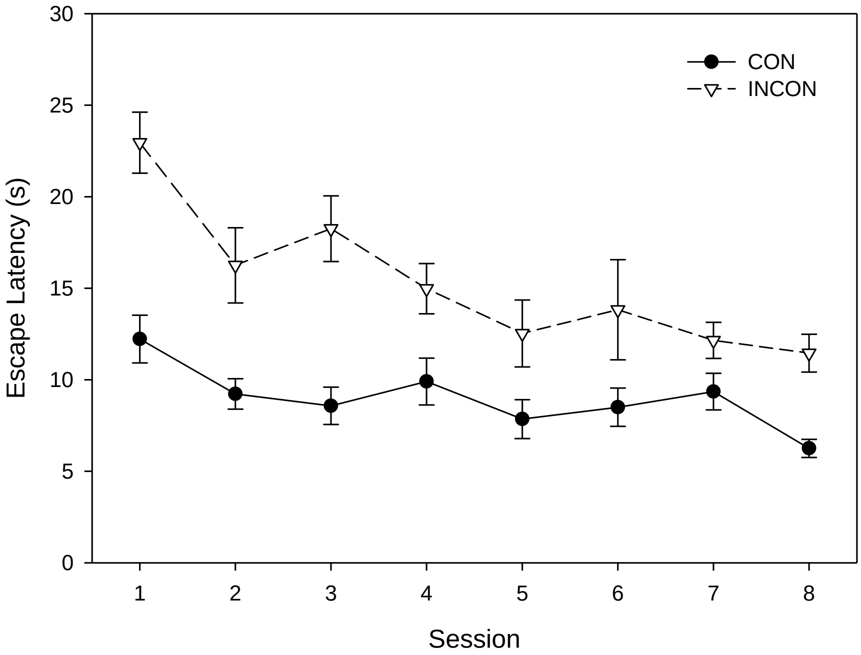


Figure 3.12: Time taken to find the hidden platform for groups CON and INCON during the revaluation stage of Experiment 2. Group NON did not participate in this stage of the experiment. Error bars represent ± Standard Error of the Mean.

interaction suggested that group CON found the hidden platform significantly more quickly than group INCON on all sessions, *F*s(1, 18) > 4.8, *p*s < .04, except six and seven, which approached significance, *F*s(1, 18) > 3.3, *p*s < .09. Both groups CON and INCON showed a decrease in time taken to find the platform from the first to last trials, *p*s < .05, indicating that both groups showed learning about the position of the platform in relation to the geometric cues during the revaluation stage. Importantly, group INCON's significant decrease in time taken to find the platform across sessions indicated that this group had learned that the previously incorrect location with respect to geometric cues was now the correct location.

3.3.2.3.2 First Choice

A second measure of the effect of the revaluation stage on groups CON and INCON analysed in which of the two non-apex corners of the triangular arena animals first searched for the hidden platform (Figure 3.13). In accordance with the time taken to find the platform, it can be seen that group CON consistently showed a high proportion of visits to the correct corner first across sessions, whereas group INCON began the revaluation stage with a much lower proportion of correct first choices than group CON, but gradually improved over time as they learned the new location of the hidden platform.

A mixed ANOVA (Revaluation x Session) showed a significant main effect of session, *F*(4.2, 75.8) = 7.44, *p* < .001, with proportion of correct first choices improving over time. There was also a significant main effect of revaluation, *F*(1, 18) = 60.6, *p* < .001, with group CON's initial visits to the correct corner being significantly higher than those of group INCON. There was also a significant interaction between

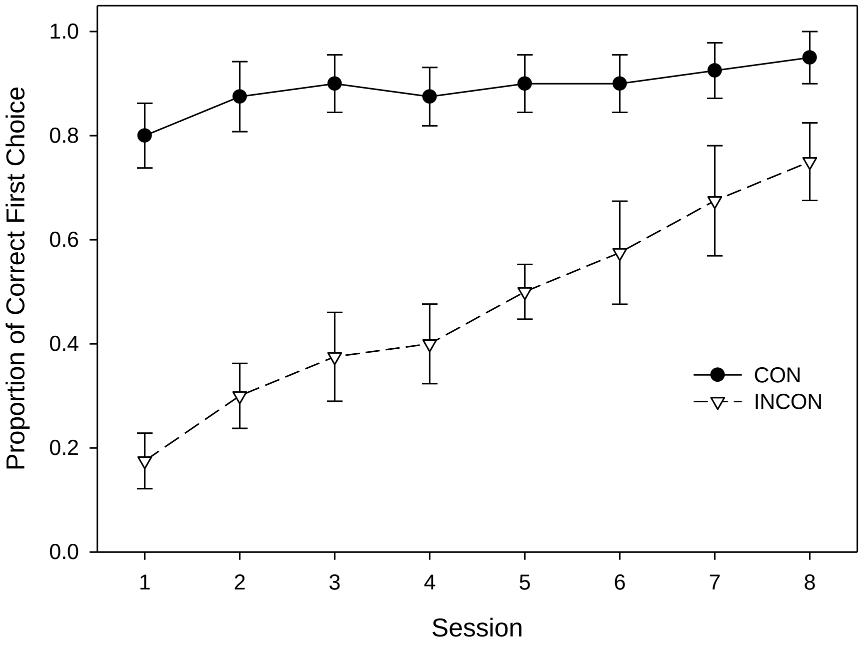


Figure 3.13: Proportion of correct first choice for groups CON and INCON during the revaluation stage of Experiment 2. Group NON did not participate in this stage of the experiment. Error bars represent ± Standard Error of the Mean.

revaluation and session, *F*(4.2, 75.8) = 3.23, *p* = .015. Analysis of the simple main effects of this interaction showed that for group CON no session saw a significantly different proportion of correct first choice than any other, *p*s > .1, whereas group INCON showed a significantly higher proportion of correct first choice for session 8 than for session 1, *p* < .001. This indicates that group INCON had improved in their choice of where they searched for the hidden platform, as a consequence of the revaluation training. Despite this improvement by group INCON, they showed a significantly lower proportion of correct first choice than group CON across all eight revaluation sessions, *p*s < .05.

The combination of the latency and first choice data for the revaluation stage strongly suggests that group INCON reversed their learning about the position of the hidden escape platform with respect to the geometric cues available. Group CON continued to demonstrate performance commensurate with that displayed at the end of the 18 sessions of compound training.

3.3.2.4 Post-Revaluation Landmark Test

A post-revaluation measure of the discrimination between landmark cues was used to determine whether the differential training during the revaluation stage had differentially affected landmark learning. It was argued in Chapter 2 that the revaluation effect, and thus the strength of the within-compound associations, between ball and geometry, and prism and geometry, were similar. Although this was not expected to be any different in this experiment, a mixed ANOVA (Zone x Revaluation x Landmark) was conducted in order to confirm this. This ANOVA showed no main effect of landmark, $F < 1$, and no interactions involving landmark, Fs < 2.17, ps > .13. Therefore, it can be concluded that the strength of within-compound associations formed between the cues were similar, following the same logic as in Chapter 2. For clarity, this landmark variable has been collapsed in further analyses of the results of this post-revaluation landmark test.

Figure 3.14 suggests that while groups CON and NON retained their ability to discriminate between the correct and incorrect landmark cues, group INCON searched for the hidden platform similarly underneath each of the landmarks. In fact, group INCON ($M = .48$ s) spent less time searching underneath the landmark cues than would be expected by chance (0.8 s), $t(9) = 2.67$, $p = .026$. This would suggest that the animals in group INCON were actively avoiding both landmark cues. It is understandable that they avoided the landmark that failed to predict the location of the hidden platform during compound training, but more informative that they also avoided the landmark

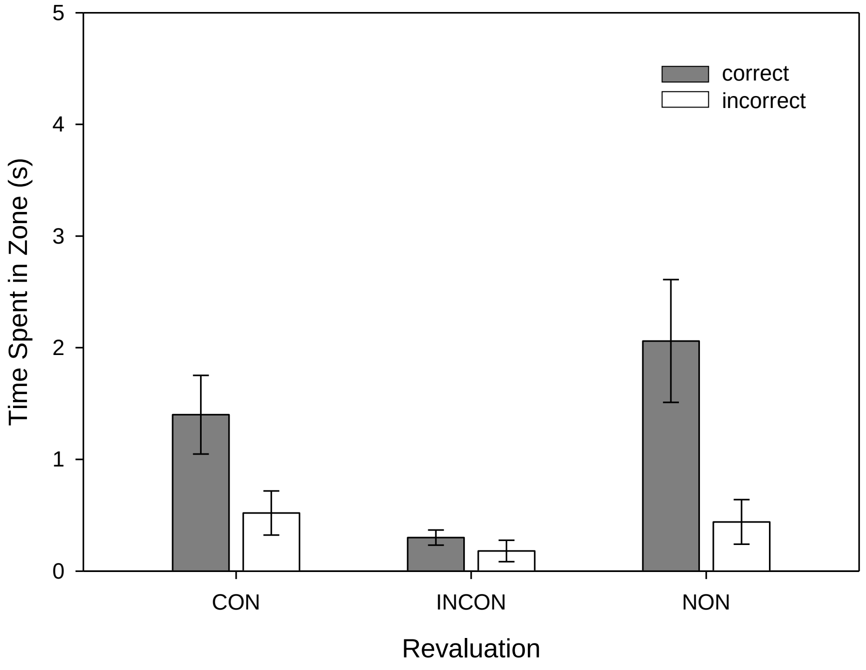


Figure 3.14: Time spent searching for the hidden escape platform underneath the correct and incorrect landmark cues during the post-revaluation landmark test in Experiment 2. Error bars represent ± Standard Error of the Mean.

that had indicated the platform's position during training. This landmark was paired with the geometric cue that was devalued during the revaluation stage. Therefore, it would appear that this geometry devaluation had affected performance towards the landmark, conceivably through the formation of a within-compound association between those cues. However, without a comparison between this group of animals and one that did not undergo geometry revaluation, it is impossible to be sure that this reduction in performance is not attributable to other factors, such as forgetting the relevance of landmark cues altogether.

A mixed ANOVA (Zone x Revaluation) of time spent searching within the zones showed a significant interaction between zone and revaluation, $F(2, 27) = 4.35$, $p = .023$. A multivariate analysis of this interaction showed that animals in group CON retained their ability to discriminate between correct and incorrect landmarks, $F(1, 27) = 5.98$, $p = .021$, as did animals in group NON, $F(1, 27) = 20.3$, $p < .001$, with both of these groups spending significantly more time searching for the hidden platform under the correct, rather than the incorrect, landmark. Those animals in group INCON failed to discriminate between the two landmarks, $F(1, 27) = .111$, $p = .741$. Univariate analysis of the Zone x Revaluation interaction shows that the groups differed in the amount of time spent searching for the hidden platform near the correct landmark, $F(2, 27) = 5.51$, $p = .010$. Pairwise comparisons of this significant effect showed that a comparison of the amount of time groups CON and INCON spent in the correct zone almost reached the required level of significance, $p = .050$, with those animals in group CON spending more time in the correct zone than group INCON. Additionally, group NON spent significantly more time searching in the correct zone than group INCON, $p = .003$, but an similar amount of time when compared to group CON, $p = .229$. All three groups spent a similar amount of time exploring underneath the incorrect landmark, $F(2, 27) = 1.07$, $p = .356$. There was a significant main effect of zone, $F(1, 27) = 17.7$, $p < .001$, with more time spent exploring underneath the correct landmark than the incorrect landmark. There was also a significant main effect of revaluation, $F(2, 27) = 5.00$, $p = .014$. Pairwise comparisons showed that animals in group CON spent a similar amount of time exploring underneath landmarks as animals in groups NON and INCON, ps > .05. Animals in group NON spent a significantly greater time near landmarks than those in group INCON, $p < .05$.

These data suggest that by revaluing the geometry cues for group INCON, the landmark cues were also revalued, such that animals failed to discriminate between the landmark under which the platform was always located during initial training, and the landmark under which the platform was never located. This failure to discriminate is contrasted with the behaviour of groups CON and NON, which both retained their ability to discriminate between the correct and incorrect landmarks. These results can be interpreted as were those of Chapter 2 Experiment 3: during the post-revaluation landmark test group INCON’s experience of the initially correct landmark evoked a representation of the geometric cue with which it was paired during training. This geometric cue had been demonstrated to no longer indicate the location of the hidden escape platform during revaluation, and hence the evoked representation prevented animals from searching underneath this landmark. Groups CON and NON did not have this evoked inhibitory representation and so retained their discrimination of the two landmark cues. These results, combined with those of Chapter 2 Experiment 3, not only confirm that within-compound associations formed between the landmark and geometry cues, but also show that experience of either cue in isolation evoked a representation of the cue with which it was paired during training. This allows within-compound associations to be the mechanism by which either landmark or geometry cues were able to counteract overshadowing of, or potentiate learning about, the other cue type, when trained in compound.

Although groups CON and NON did not differ statistically in their discrimination of landmarks, the numerical advantage conferred to group NON may be a suggestion that the within-compound associations formed between landmark and geometry cues for group CON were weakened as a consequence of the revaluation training. During the revaluation, the geometry cues were presented in the absence of the landmark cues, thus conceivably weakening the association between landmark and geometry. The presentation of only one cue of a compound of cues has previously been shown to weaken the within-compound association between those cues (e.g., Rescorla & Freberg, 1978) and this could account for any worsening of performance that group

CON might experience, despite still being rewarded for the geometry component of the landmark-geometry compound.

3.4 General Discussion

In Experiments 1A and 1B it was shown that geometric cues did not overshadow learning about landmark cues. This apparent lack of cue competition between geometry and landmark reflects similar findings by McGregor et al. (2009) and Horne and Pearce (2011). However, in contrast to Horne and Pearce, a lack of overshadowing is observed regardless of the salience of the landmark cue, about which more will be discussed shortly. Experiment 2 demonstrated that the within-compound associations present between landmark and geometry cues are a plausible mechanism by which the lack of overshadowing of landmark cues by geometry occurred. The experience of the correct landmark during the test evoked a representation of the correct geometry with which it was paired during compound training, thus boosting discrimination between correct and incorrect landmarks.

As there was no difference between the levels of revaluation depending on which landmark cue was correct it could be assumed that there was no difference in the strength of the evoked representations of landmarks, and thus of within-compound associations. This is similar to what was observed in Chapter 2 Experiment 3, that the within-compound associations formed between landmark and geometry cues were of similar strengths. Therefore, the level of overshadowing of the two landmark cues by geometry must have been similar, regardless of the salience of the landmark cue, as the identity of the landmark did not affect the level of cue competition observed. That geometry failed to overshadow learning about landmark regardless of the salience of the landmark cues would seem to suggest that the salience of the geometry cues was relatively dissimilar to that of the landmark cues. This would have induced either very strong, or very weak, overshadowing of the landmark cues by those geometry cues, dependent on whether the geometry cues were substantially more or less salient than the landmark cues, respectively. It is difficult to more than speculate about which of these is the more likely explanation as the actual strength of the evoked representation of landmark cues that the within-compound associations facilitate was not determined. If the evoked representation of the landmark cues was strong, then a high degree of overshadowing could be counteracted by the presence of within-compound associations. However, a weakly evoked representation of the landmark cue might only be capable of counteracting a weak overshadowing effect caused by geometric cues of much lower salience than the landmark cues.

It could be argued that the failure to observe overshadowing of landmarks by geometry in Experiments 1A and 1B is explicable by appeal to Mackintosh (1976). If the geometry cues were of lower salience than the landmark cues then it would be expected that geometry would fail to overshadow learning based on the landmarks. Mackintosh would predict that this salience difference would result in minimal learning about the geometry cues. However, Figure 3.13 shows that group CON, even during the first session of revaluation, located the platform quickly, indicating that those animals had learned about the geometry cues during compound training. In addition, if the geometry cues were of a low salience compared to the landmark cues then Mackintosh would predict overshadowing of geometry by landmark, the opposite to that which was observed in Chapter 2. While Mackintosh fails to explain these results, and the potentiation of landmarks by geometry observed by McGregor et al. (2009), within-compound associations can readily account for these observations.

Whilst it has been argued that the presence of within-compound associations, and the evoked representations of landmarks that they afford upon experience of the geometric cues, explains the reason for the failure to observe overshadowing, other explanations have been put forward, which do not require the presence of within-compound associations. There has been proposed a module dedicated to processing information about geometric features of the environment (Cheng, 1986; Gallistel, 1990). One feature of this module is its impenetrability to non-geometric information. It would therefore be no surprise that landmark cues are not overshadowed by geometry, as learning about these two types of cue would be predicted to occur separately. However, this explanation would not allow the formation of within-compound associations between the landmark and geometry cues that resulted in the revaluation effects demonstrated in this, and the previous, chapter. This geometric module would also allow neither the potentiation seen in Chapter 2, nor the accounts of discrete landmarks competing with geometric cues demonstrated elsewhere (e.g., Kosaki et al., 2013).

A further theory behind the absence of cue competition between landmark and geometric cues comes from Timberlake, Sinning, and Leffel (2007). They proposed that learning with respect to cues occurs more rapidly if a stable framework has already been learned, against which these new cues are introduced. In Experiments 1A and 1B, the presence of a stable framework of geometric cues provided by the shape of the arena for the compound groups might have allowed learning with respect to the landmark cues to occur more rapidly compared with the control groups, which did not have this stable framework of geometric cues. Therefore, potentiation of landmark learning, as a consequence of the framework of geometric cues, would be predicted by this theory. However, Experiments 1A and 1B did not demonstrate potentiation of landmark learning, only a failure of geometric cues to overshadow the landmarks. It should also be noted that this theory predicts more rapid learning against a stable framework of cues. However, the data from the training sessions of Experiments 1A and 1B showed that, although group compound may have shown lower latencies to find the hidden platform than group landmark overall, the rate at which these two groups learned about the location of the hidden goal was not different, as indicated by the lack of a significant interaction between the session and group variables. It seems, therefore, that Timberlake et al.’s stable framework theory cannot explain the failure to observe cue competition between landmark and geometry cues in this chapter. In addition, although potentiation of geometry learning by concurrently trained landmark cues was observed in Chapter 2, Timberlake et al. cannot convincingly explain this either. For their theory to apply to these results, geometry learning would need to have progressed more rapidly due to a stable framework provided by the two distinct landmark cues in the compound groups. The control groups, which did not experience a stable framework of landmark cues, would be expected to learn about the geometric cues at a lower rate. However, as with Experiments 1A and 1B, the rate of learning was similar between those animals trained with this stable framework of landmark cues, and those trained in its absence. It is therefore unlikely that a theory based upon a stable framework of cues facilitating learning can explain any of the failures of cue competition demonstrated in Chapters 2 and 3.

Within-compound associations appear to present the most convincing mechanism by which either a lack of cue competition, or potentiation of one cue by another, can occur in spatial learning. A reciprocal failure to overshadow between landmark and geometry cues has been shown, and it has also been demonstrated that these cues enter into within-compound associations such that either cue can evoke a representation of the other, and that this evoked representation is strong enough to influence behaviour. Admittedly, a causal, rather than correlational, link between failure to observe overshadowing and within-compound associations would provide stronger evidence for the implication of within-compound associations in these effects. One such causal procedure may involve abolition of the within-compound associations formed between concurrently trained cues in an attempt to reinstate the expected overshadowing effect. One way to weaken these within-compound associations is through repeated presentations of one cue in the absence of the cue with which it was paired, as discussed previously. Although this afforded no significant decrease in within-compound association strength in Experiment 2, as evidenced by groups CON and NON discriminating similarly between correct and incorrect corners, group CON showed a potential weakening of within-compound associations as a result of repeated presentation of geometric cues in the absence of landmark cues. This suggests that further elemental training may have allowed the within-compound associations to be significantly weakened and eventually abolished. To demonstrate a causal link between failure to observe cue competition and within-compound associations, two groups of animals would need to be trained. One group would be trained to locate the hidden platform with reference to a compound of geometry and landmark cues (group compound). The other would be trained with only geometry cues relevant for finding the platform, with ambiguous landmark cues (group control). These two groups are analogous to those of Chapter 2 Experiment 2, in which potentiation of geometry learning by landmarks was demonstrated. After training, both of these groups would undergo landmark training in the absence of geometric cues. For both groups only the landmark cue that indicated the presence of the platform during training would be present, again with the platform underneath. This elemental training would serve to reduce the strength of the within-compound association formed between this landmark and the geometric cue with which it was paired during training. Following this elemental training, both groups of animals would then undergo a geometry test in the absence of the landmark cues and the hidden platform. Had within-compound associations been abolished by the elemental training, and if within-compound associations are the cause of failures to demonstrate cue competition, it would be expected for the control group to show better discrimination between the correct and incorrect geometric cues than the compound group. This would constitute a reinstatement of overshadowing of geometric cues by the presence of the discriminable landmark cues through abolition of the within-compound associations. However, until a successful demonstration of this causal link is shown, the experiments in this chapter, combined with those discussed previously in Chapter 2, present the clearest evidence that within-compound associations are a plausible mechanism for the common apparent failure to find cue competition between spatial and non-spatial cues.

CHAPTER FOUR

Within-compound Associations in Humans

In Chapters 2 and 3, within-compound associations were implicated in the frequent failure to observe overshadowing of both geometric cues by landmarks, and of landmark cues by geometry. Whilst these failures to overshadow are much less prevalent in the human literature, recent work by Redhead, Hamilton, Parker, Chan, & Allison (2012) has shown results very similar to those observed in rats. In a virtual Morris Water Maze (MWM), the position of a hidden platform was indicated by both a beacon and the shape of the pool. In one experiment, Redhead et al. demonstrated that learning about the shape of the pool was overshadowed by the presence of the beacon when the pool was a trapezium, but not when it was an isosceles triangle. Their second experiment ruled out the possibility of this overshadowing effect being due to generalisation decrement by introducing a second beacon, placed in another location within the pool. For the overshadowing group the two beacons were distinct, but for the control group they were identical. In a further experiment, it was shown that the lack of overshadowing of the triangular arena was not because the geometry was more salient than the beacon. The authors conclude that associative processes cannot fully explain cue competition between spatial and non-spatial cues. However, this is not the only explanation of their results. From the results of Chapter 2 it is evident that the presence of within-compound associations formed between geometric and non-geometric cues can account for this failure of a landmark cue to overshadow learning about the geometry. However, this calls into question why overshadowing occurs when the arena is shaped as a trapezium, but not as a triangle. Redhead et al. state that the longer escape latencies found for the control group trained in the trapezium, compared with those trained in the triangle, implies that the trapezium provided less salient geometric information than the triangle. Very similar logic to that discussed in Chapter 2 can be applied to explain why differential overshadowing might be observed as a result of within-compound associations. As the triangular arena is a more salient geometric cue, it will be overshadowed less by the beacon than would the trapezium arena. Therefore, the boost in responding to geometry in the triangular arena during test afforded by the within-compound associations may be enough to counteract any overshadowing effect that would have been present. Conversely, it would be expected that the less salient trapezium geometry would be overshadowed more strongly by the beacon such that the presence of the within-compound associations was able only to weaken, but not remove, this strong overshadowing effect. It is therefore entirely plausible, given what has been learned about the action of within-compound associations from the previous experiments reported in this thesis, that Redhead et al.'s results in humans are explicable in exactly the same manner as similar failures to observe overshadowing in rats.

The presence of within-compound associations has been demonstrated in a variety of tasks in humans (e.g., Dickinson, 1996; Dickinson & Burke, 1996; Vadillo, Castro, Matute, & Wasserman, 2008; Wasserman & Berglan, 1998). However, very few studies have demonstrated that humans are able to form within-compound associations between cues of a spatial nature. One such study, conducted by Prados, Alvarez, and Reynolds (2011), presented geometric and non-geometric cues in compound, after pre-training with one of those cues. Testing the cue that had never been presented with reinforcement demonstrated a second-order conditioning effect, with participants searching preferentially near the cue that had been paired with the pre-trained cue. Additionally, initial presentation of the compound of geometric and non-geometric cues was followed by reinforcement of one of the cues. Testing the non-reinforced cue demonstrated a sensory preconditioning effect, with participants again searching preferentially near the cue paired with the reinforced cue. These two experiments suggest that within-compound associations had formed between the geometric and non-geometric cues. However, these experiments were not conducted in a manner very similar to those of Redhead et al. (2012). They were more akin to traditional pencil-and-paper tasks, albeit the cues were presented on a computer screen. Unlike experiments utilising a 3-dimensional representation of the environments, the geometric and non-geometric cues in the study by Prados et al. were presented in 2-dimensions with the geometric cues provided by a rectangle and the non-geometric cues provided by the colours of the sides of this rectangle. Before critiquing this methodology, some of the difficulties facing experimenters in their attempts to develop human spatial learning tasks analogous to those used in rodents should be explored.

One major issue when designing a human spatial learning experiment is that the large environments required are often familiar to the participants, mostly occurring within university campuses or the surrounding neighbourhood (Abu-Ghazzeh, 1996; Bell & Saucier, 2004; Foreman, Stanton-Fraser, Wilson, Duffy & Parnell, 2005; Kozlowski & Bryant, 1977; Passini, Rainville, Marchand, & Joanette, 1995). Whilst there have been some attempts to overcome this problem by using large purpose-built apparatus to approximate a MWM for humans (e.g., Overman, Pate, Moore & Peuster, 1996), it remains difficult to have complete control over the large global cues often present in our environments. Real-world navigation, as in these examples, also restricts tasks to those solely based on behaviour. It is beyond current technology to conduct brain-imaging studies outside of the laboratory, whereas it is precisely these kinds of studies that are required to demonstrate that the vast quantity of knowledge regarding the neurological aspects of spatial learning already elucidated from animal studies is transferable to humans. Tasks requiring navigation through large virtual environments are also restrictive in terms of viable participants. Older people, whose abilities in spatial learning may be very important to study in relation to the variety and prevalence of degenerative neurological conditions, may be less able to complete these tasks than younger people due to deterioration in physical, rather than mental, ability.

One possible solution to the problems posed by conducting spatial learning tasks in a real-world environment is to use 2-dimensional pencil-and-paper tasks. Experimenters can have absolute control over the information provided to participants in this type of task, and studies can be completed within a laboratory setting for a wide range of participants. These pencil-and-paper tasks can take many forms, such as mental rotation (e.g., Shepard & Metzler, 1971), memory of object location (e.g., Silverman & Eals, 1992), or route-learning through a town (e.g., Galea & Kimura, 1992). However, these tasks are often confounded by variations in participants' abilities to draw, map-read, or communicate effectively what they have learned. There are also major differences between real-world and pencil-and-paper tasks in terms of both the participant's perspective, and their frame of reference. During real-world navigation, participants inhabit the environment and view it from a first-person perspective, whereas in a pencil-and-paper task they are outside of the environment, viewing it from an aerial perspective. As such, it has been argued that while much may have been learned about human spatial learning from these tasks, the cognitive processing required to complete them is not comparable with that of navigation through a real-world environment (Hegarty, Montello, Richardson, Ishikawa & Lovelace, 2006).

Given these criticisms levied against pencil-and-paper studies of human spatial learning as to how accurately they approximate real-world spatial learning, it would be premature to assume that, from the study conducted by Prados et al. (2011), humans are able to form within-compound associations between geometric and non-geometric cues in much the same manner as observed in rats in Chapters 2 and 3. In order to assert that the presence of within-compound associations between geometric and non-geometric cues is the cause of the failure to observe overshadowing of geometric cues in the study by Redhead et al. (2012), a demonstration of the presence of these within-compound associations in a 3-dimensional environment is necessary.

One way in which it is possible to overcome many of the problems associated with studying human spatial memory in real-world, and pencil-and-paper, tasks is afforded to us by the relatively recent advances in technology allowing the display of virtual 3-dimensional environments to participants. Experimenters can have much greater control over this virtual environment, compared with the control that is possible over a real-world environment. Participants are able to navigate within these environments using a joystick or keyboard, and often have to locate a hidden goal, in a similar manner to rats in a MWM. Virtual environments have been used extensively to investigate spatial learning in humans, using analogues of the MWM (e.g., Astur, Ortiz, & Sutherland, 1998; Hamilton, Driscoll, & Sutherland, 2002; Hamilton & Sutherland, 1999; Sandstrom, Kaufman, & Huettel, 1998), radial arm maze (e.g., Astur, Tropp, Sava, Constable, & Markus, 2004; Levy Astur, & Frick, 2005), enclosed geometric arenas (e.g., Kelly & Bischof, 2005), and open-field environments (e.g., Doeller & Burgess, 2008). A variety of studies have been conducted into the efficacy of learning within these virtual environments, and whether they parallel real-world learning. Rose, Attree, Brooks, Parslow and Penn (2000) claimed that transfer of learning from a virtual-to-real environment was at least as good as transfer from a real-to-real environment. Additionally, Waller, Hunt, and Knapp (1998) demonstrated superior learning from a virtual environment when compared with a real environment, given sufficient training. Richardson, Montello, and Hegarty (1999) concluded that, although they did not find exact agreement between spatial representations learned from virtual and real-world environments, the cognitive processes involved in both types of navigation were similar (see also Ruddle, Payne, & Jones, 1997).

With Redhead et al. (2012) failing to demonstrate overshadowing of geometry learning by landmarks in a triangular-shaped arena, this would have been the obvious place to look for the presence of within-compound associations, which may have counteracted any overshadowing. Participants were trained to locate a hidden goal with respect to a compound of landmark and geometry cues in an isosceles triangular-shaped arena. The landmark cues and hidden goal were then removed for a single trial to determine how much had been learned about the geometry cues. It was found that nothing had been learned about the relationship between the geometry cues and the goal location, with participants searching for the hidden goal similarly near each geometric cue. With no geometry learning occurring as a result of the compound training, it would have been impossible to determine the presence of within-compound associations between the geometry and landmark cues. The design of Experiment 1 is the result of a protracted process to establish a paradigm under which learning about geometric cues occurred when participants were trained with a compound of geometry and landmark cues. In this design, neither the landmark cues nor the geometry cues indicated the location of the hidden goal on their own, participants were required to use both cues to locate the hidden goal in each trial. This served to reduce the potential competition between these two cues, increasing the amount learned about the geometry cues as a consequence. With both geometry and landmark cues being learned about during compound training, the presence of within-compound associations between these two cues could be determined.

During the process of developing a viable paradigm for the study of within-compound associations between geometry and landmark cues in humans, it became clear that there were robust differences in the abilities of males and females to complete these tasks. Males tended to show lower latencies to find the hidden goal during compound training. Males also discriminated more strongly between geometric cues immediately following compound training, suggesting that they had learned more about the geometric cues than females. As such, the following experiments will introduce gender as a variable in order to determine whether these apparent differences affect the formation of within-compound associations.

4.1 Experiment 1

To demonstrate the presence of within-compound associations between landmark and geometric cues in a task similar to that used by Redhead et al. (2012), a fully-customizable set of virtual environments was developed. Participants could navigate within these environments in the first person to locate a hidden goal with reference to non-geometric cues provided by objects within the environment, and geometric cues provided by the shape of the environment. Learning could be assessed through two measurements: time taken to find the hidden goal, and amount of time spent searching for the hidden goal in the proximity of certain cues. In this manner, it was possible to approximate the MWM for human participants, in a fully controlled environment.

The previous demonstrations of within-compound associations relied on the comparison of two groups of differently trained animals. Both groups were trained to find a hidden platform by reference to a compound of geometric and non-geometric cues. However, one group of animals then experienced a revaluation of the non-geometric cue, which in turn revalued the geometric cue. The other group experienced no such revaluation, and retained a preference for the initially trained geometric cue. It was assumed for these experiments that the two groups of animals were functionally identical: they were of the same age, sex, and strain, from the same breeder, and housed in the same conditions. Unfortunately, the same control cannot be ensured over human participants. For this reason, and to bypass any potentially confounding individual differences, the between-subjects design used successfully in our animal experiments was adapted to allow a within-subjects demonstration of within-compound associations in humans. Participants were initially trained to locate a hidden goal by way of two distinct compounds of geometric and non-geometric cues, presented in separate trials.

Geometric cues were provided by two distinct corners of a trapezium-shaped arena. The non-geometric cues were two discriminable floating cubes. Following training to these distinct compounds, the landmark cues were then presented in the absence of the geometric cues, with one landmark cue still indicating the goal’s location, while the other indicated its absence. The effect of this landmark revaluation was then tested by removing the landmark cues and measuring the participants’ preference for the geometric cues. Should within-compound associations form between geometric and non-geometric cues in humans, each geometric cue should evoke a memory of the landmark cue with which it was paired during training. It would therefore be expected that participants would avoid the geometric cue associated with the revalued landmark cue. Instead, they should show a preference for the geometric cue associated with the landmark that still indicated the presence of the goal during the revaluation stage. This would be analogous to the animal results demonstrated earlier, with those animals undergoing no revaluation of the landmark cue retaining a preference for the concurrently trained geometric cue.

4.1.1 Method

4.1.1.1 Participants

There were 24 participants in this study, eight of whom were male. Ages ranged from 18-33. There was no significant difference between the ages of males (M = 22, SD = 5) and females (M = 19, SD = 2), $t(22) = 1.80$, $p = .085$.

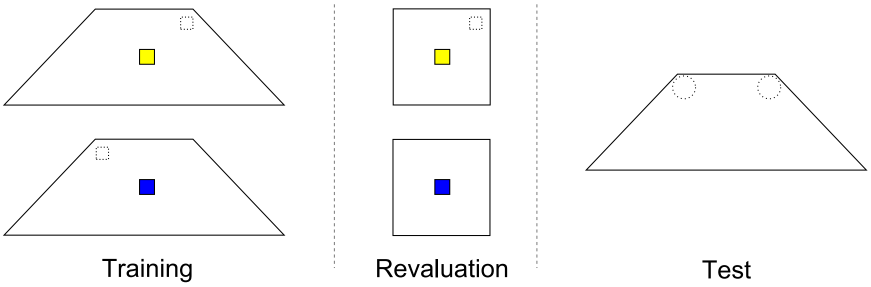
4.1.1.2 Apparatus

Custom software was used to present 3D virtual environments to participants, at a resolution of 1024 x 768 pixels on a flat-screen monitor. A series of trials were presented, in which participants were placed into a variety of arenas, which were viewed from a first-person perspective. The floors of these arenas were textured to look like grass, and the view beyond the arena textured to appear as sky. Although no arenas were surrounded by visible walls, invisible barriers prevented participants from falling off the edge of each arena. All training trials, and the test trial, occurred within a trapezium-shaped arena. The parallel sides of this trapezium were 6.4 m and 19.2 m long, separated by a distance of 6.4 m. The two non-parallel walls were both 9.1 m in length. Revaluation trials occurred within a square-shaped arena, with a side-length of 3.8 m. Participants could move within these arenas at a speed of 1.8 m/s, approximating a brisk walking pace. The view of the arena could be rotated such that a single 360° rotation took 6 s. There were two landmark cues used in this experiment. Both of these landmarks were cubes of side length 48 cm, with one landmark being blue, and the other yellow. During training and revaluation, one of these landmark cues floated above the very centre of the arena, at a height such that the participant could just move underneath the landmark without making contact. During all training trials, and some revaluation trials, there was a hidden goal present within the arena. This goal was a square, with side-length 64 cm. During the training trials it could be located towards either end of the shorter of the two parallel sides of the trapezium-shaped arena. At whichever end of the shorter side it was located, the centre of the goal was 72 cm from the shorter of the parallel sides, and 104 cm from the nearest non-parallel side. During the revaluation trials in which it was present, the goal was located in one corner of the square-shaped arena, such that its centre was 72 cm away from two adjacent sides of the arena. A marker indicating the position of this hidden goal was presented to participants who did not find the goal in any trial in which a goal was present. This marker was a black cylinder, of diameter 8 cm and height 3 m, which appeared at the centre of the goal location once the allotted trial time had elapsed and remained until the participant had made contact with the hidden goal.

4.1.1.3 Procedure

The experiment consisted of 16 training trials, eight revaluation trials, and a single test trial. A schematic representation of this design can be seen in Figure 4.1.

a.



b.

Figure 4.1: A not-to-scale schematic of the design for Experiment 1 (a) and a participant's view of the arena during training (b). Yellow and blue squares represent the yellow and blue landmarks, and the dashed outline of a square represents the presence and location of a hidden goal.

During the training stage, participants were given 16 trials in which one of two distinct landmark cues was present in the centre of the trapezium-shaped arena. The identity of the landmark cue indicated the location of the hidden goal during that trial, with the goal being located at either end of the shorter of the two parallel sides of the arena. Each landmark was presented eight times, with the participant beginning each of these trials at the centre of one of the sides of the arena, facing towards the landmark. Each of the four sides of the arena was used as a starting point twice for each landmark cue. The relationship between the identity of the landmark and the location of the hidden goal was counterbalanced between participants, such that for half of the participants the yellow landmark indicated that the goal was to the right-hand end of the shorter parallel side, whereas the rest of the participants found the goal in this location on those trials in which the blue landmark was present. Participants were allowed 120 s to locate the hidden goal in each training trial. If a participant had not found the goal before this time had elapsed, a marker appeared in the centre of the goal location, with an onscreen message instructing participants to navigate to it. Once the participant had made contact with the goal, a congratulatory message appeared onscreen, with a 10-s countdown to the next trial. During this time the participant’s movement was disabled, but they were able to rotate their view to aid in learning the location of the hidden goal.

During each of the revaluation trials, one of the landmark cues was presented in the centre of a square-shaped arena. Participants could therefore not use the shape of the arena to locate the hidden goal, only the identity of the landmark. Each landmark cue was presented four times during this revaluation stage, with the participant beginning each of the eight revaluation trials in the centre of one of the four sides of the arena, facing towards the landmark. Each of the four sides was used as a starting point for two revaluation trials, one containing each landmark. When one of these landmark cues was presented, the hidden goal was also present. However, on trials containing the other landmark cue, the hidden goal was absent. The relationship between the identity of the landmark and the presence or absence of the hidden goal was counterbalanced between participants. Revaluation trials in which the hidden goal was present proceeded in exactly the same manner as the training trials. On those trials with the goal absent, after 60 s had elapsed the participants were informed that they had not found a goal during this trial, and the 10-s countdown to the next trial began. The contingency of the first trial of the revaluation stage was counterbalanced, such that for half of the participants the goal was present during this first trial, and for the rest the goal was absent.

Participants began the test trial in the centre of the longer of the two parallel sides of the trapezium-shaped arena, facing towards the centre of the arena. They were given 60 s during this test trial to search for the hidden goal. There were no landmark cues present during this test trial, and as such participants were required to use only the shape of the arena to determine where they thought that the hidden goal should be located. The time spent searching for the goal in two circular zones was calculated. These zones were 1.5 m in diameter with their centres coincident with the centres of the hidden goals during training.

4.1.2 Results and Discussion

4.1.2.1 Training

In order to measure learning during the training trials, the time taken to locate the hidden goal in each trial was recorded. Latencies were recorded as a mean of four consecutive trials to equate the distance from the starting position to the goal location. In addition, to ensure that both landmark-geometry cue compounds were learned equally well, the training trials were split by which cue compound was present. The latency data from this training stage can be seen in Figure 4.2. It is apparent that over the course of the training stage of this experiment males required less time to locate the hidden goal than females. The time taken to find the goal appears to be lower for the second block of trials, with both males and females decreasing their latencies to find the goal to a similar degree. It should be noted that although trials are split by those containing the landmark to be revalued and those containing the landmark that will continue to indicate the goal's location, this differentiation refers to the subsequent revaluation stage. It is therefore no surprise that performance during training is not affected by this differentiation.

A mixed model ANOVA (Compound x Trial Block x Gender) supported these observations, with significant main effects of trial block, $F(1, 22) = 43.6$, $p < .001$, and

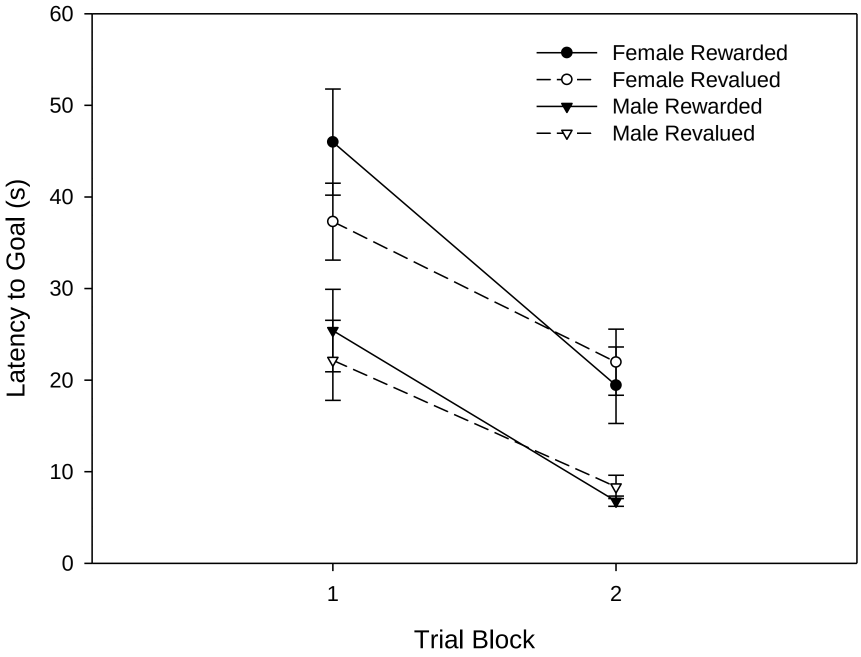


Figure 4.2: The time taken to find the hidden goal during the training stage of Experiment 1. Trials are split by those containing the landmark that is to continue to indicate the location of the goal during revaluation, and those containing the landmark to be revalued.

gender, $F(1, 22) = 9.50$, $p = .005$. No other main effects, and no interactions, were significant, $F\text{s} < 1.91$, $p\text{s} > .18$. An overall decrease in the time taken to locate the hidden goal suggests that both males and females learned to more accurately pinpoint its location as training progressed. That males consistently found the platform more quickly than females suggests either that they had learned more about the location of the goal, or that males were just more proficient at moving around within the environment, possibly relating to experience with this type of apparatus.

4.1.2.2 Revaluation

A hidden goal was present on only half of the revaluation trials, with the starting location of each of these trials at a different one of the four identical sides of the square arena. The distance between the starting location and the hidden goal was therefore not equated between trials, and so comparisons between trials would not be appropriate. However, the time taken to locate the hidden goal between males and females during this revaluation stage can be compared. An independent samples t-test showed that males ($M = 14.9$ s, $SD = 9.8$) and females ($M = 17.9$ s, $SD = 8.0$) did not differ in their average time to locate the hidden goal across these revaluation trials, $t(22) = 0.81$, $p = .43$. It is difficult to conclude too much about the effect of the revaluation stage of training from these data, especially given the difficulty in quantifying the extinction afforded upon the devalued landmark.

4.1.2.3 Geometry Test

The amount of time spent searching for the hidden platform in each of the two geometric locations – either end of the shorter of the parallel sides, coincident with the locations of the hidden goals during training – can be seen in Figure 4.3. Whilst females appear to have spent an similar amount of time searching for the hidden goal in each location, males spent more time searching for the goal near the geometric cue paired with the landmark cue that continued to indicate the presence of the goal during revaluation. Both genders appear to have spent a similar amount of time searching for the hidden goal within the zones of interest.

A mixed model ANOVA (Zone x Gender) confirmed these observations. There was a significant main effect of zone, *F*(1, 22) = 13.2, *p* = .001, with more time being spent searching for the hidden goal in the zone associated with the rewarded landmark. There was no main effect of gender, *F*(1, 22) = .048, *p* = .83, suggesting that males and females spent a similar proportion of their time during the test trial within the two zones

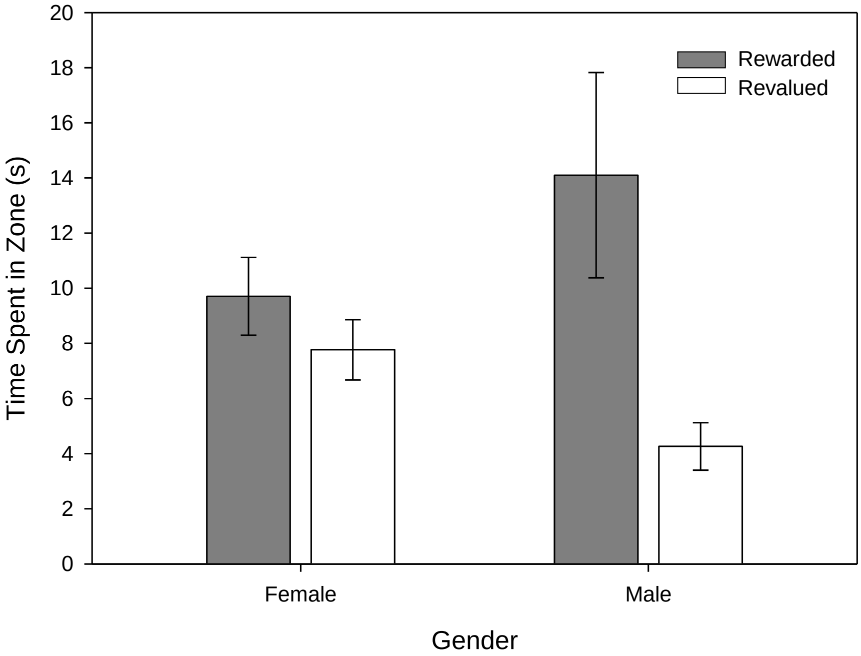


Figure 4.3: Time spent in the proximity of the geometric cues during the test trial of Experiment 1. Data are split into rewarded (geometric cue was paired with the landmark cue that continued to be rewarded during revaluation) and revalued (geometric cue was paired with the landmark cue that was revalued during revaluation). Error bars represent ± the Standard Error of the Mean.

of interest. A significant interaction between zone and gender, *F*(1, 22) = 5.95, *p* = .023, suggests that discrimination between the zones associated with the rewarded and revalued landmarks was not equal between the genders. Analysis of the simple main effects of this interaction shows that males discriminated between these two zones, spending significantly more time searching for the hidden goal in the zone associated with the rewarded, rather than the revalued, landmark, *F*(1, 22) = 13.8, *p* = .001. However, females spent a similar amount of time in these two zones, *F*(1, 22) = 1.07, *p* = .311. Whilst there was no difference in the amount of time spent in the zone associated with the rewarded landmark by the two genders, *F*(1, 22) = 1.81, *p* = .193, females spent significantly longer in the zone associated with the revalued landmark than males, *F*(1, 22) = 4.41, *p* = .048.

Greater exploration of either one of the zones of interest would suggest the presence of within-compound associations having formed between the landmark cues and the arena’s shape during the training stage. As both geometric locations were equally rewarded during training, any preference would be the result of the revaluation stage differentially associating the landmark cues with the presence of the goal. As discussed in Chapters 2 and 3, the experience of a geometric cue during the test trial could evoke a memory for the landmark cue with which it was paired during training. If this landmark had been recently associated with the absence of the goal, then the geometric location with which it was paired may be avoided. Conversely, if this landmark cue had recently been associated with the presence of the goal then its associated geometry cue may be approached. This interpretation fits the data from the male participants of this experiment, who spent more time searching for the hidden goal near the geometric cue that had previously been paired with the landmark cue that was associated with the hidden goal during revaluation. It is conceivable that the opposite could have occurred, with more time being spent searching for the hidden goal near the geometric cue associated with the landmark cue that had indicated the absence of a goal during revaluation. This would have constituted a form of retrospective revaluation of the geometry cue, such that the landmark cue’s lack of association with the goal caused the geometry-goal association to be strengthened. Although this effect would still have implied the presence of within-compound associations between landmark and geometry cues, that this did not occur suggests that the males in our experiment showed a similar revaluation effect to that observed in rats in Chapters 2 and 3. Therefore, in tasks that require learning based on both geometric cues and discrete landmarks, it would appear that the reward association afforded to one of the cues of a compound is applied in the same direction to the other cue of that compound, for both male humans and male rats.

The lack of a difference between the time spent in each of the zones for females could indicate several differences between male and female learning with respect to geometric and landmark cues. One explanation, rooted in recent literature, is that females are unable to learn about geometry as well as males (Rosenthal, Norman, Smith, & McGregor, 2012). If females were unable to learn the locations of the hidden goals during the training stage of this experiment based upon the arena’s geometric properties, then they would be unable to express any preference based on geometry during the test trial. The training data provide some evidence against this argument, however, with females showing a decrease in latency to find the hidden goal in line with that of males. This would indicate that both males and females have learned something about the location of the hidden goal. However, although this reduction in time taken to locate the goal is similar between genders, it should be noted that this does not necessarily indicate that both males and females have learned a similar amount about the location of the hidden goal. It is feasible to conjecture that the reason females took longer than males to find the hidden goal is a consequence of how accurately they were able to learn the location of the goal. It is possible that males had learned the exact geometric location of the hidden goal, whereas females had learned only that the goal was located near the shortest wall of the trapezium-shaped arena. For both genders this information should serve to reduce the time taken to locate the goal, but would strongly suggest that males had learned more about the location of the goal with respect to the shape of the arena. It could be argued that the apparent gender difference occurred as a consequence of differences in learning during the revaluation stage. Although it is not possible to show that extinction was similar between the genders, the lack of a difference between males and females in time taken to find the goal during rewarded trials helps to alleviate any concerns that the difference in performance during the geometry test was a result of differences during revaluation.

There is a second, perhaps more obvious, explanation as to why females express no geometry preference during the test trial. Had females been unable to form within-compound associations between the geometry and landmark cues during training, then the revaluation stage, during which landmark cues are trained in the absence of geometry, should have had no effect on their geometry preference. During the test trial, they would therefore explore the geometry cues to match with the geometry-goal associations formed during training. As both geometric cues had been equally associated with the hidden goal, this would manifest as equal exploration of the geometric cues at test. In order to rule out this explanation for the failure of females to discriminate between the geometric cues, it would need to be demonstrated that females are able to form within-compound associations between cues with which there is no evidence of inferior learning when compared with males. A demonstration of within-compound associations between two non-spatial cues would suggest that the reason for the lack of discrimination between geometry cues during this experiment was not because females cannot form within-compound associations between cues, but that these within-compound associations were unable to form because of comparatively retarded learning as a consequence of the nature of the cues used.

4.2 Experiment 2

The reason for females being unable to form within-compound associations between the geometric and non-geometric cues used in Experiment 1 may not be because of the nature of the cues involved. Many studies have demonstrated the presence of within-compound associations in causal judgement learning, however these have typically failed to mention whether this learning is similar between males and females. Indeed, many fail to report the genders of the participants involved (e.g., Dickinson & Burke, 1996; Wasserman & Burglan, 1998). Although it appears that females are able to form within-compound associations in causal judgement learning (e.g., Melchers, Lachnit, & Shanks, 2004), it is important to demonstrate that their inability to form these associations in Experiment 1 is not a function of the apparatus used. To my knowledge, there have been no demonstrations of within-compound associations in females (or, indeed, in males) from a task involving first-person navigation through a virtual environment. Therefore, showing that females are able to form associations in this type of task is vital for understanding the reasons behind the gender differences observed in Experiment 1.

A pilot experiment was conducted that utilized the same hidden goal paradigm as in Experiment 1, but replaced the geometric cues with non-spatial ones, which indicated the presence of a hidden goal by their visual features rather than by their locations. However, this experiment failed to elicit any meaningful searching for the hidden goal during the final test trial. Participants were trained in a very similar manner to the previous experiment, with the exception that two compounds of non-spatial cues indicated the location of the hidden goal during separate trials. One of these non-geometric cues then underwent revaluation, such that it no longer predicted the presence of the hidden goal, while the other retained its relationship to the goal. At test, the two non-geometric cues not presented during revaluation were presented in conflict, to determine whether participants demonstrated the presence of within-compound associations and preferentially explored the cue concurrently trained with the non-revalued cue. This test trial must proceed in the absence of the hidden goal in order for participants to spend time searching for it. However, likely because the non-geometric cues so accurately predicted the location of the hidden goal during training, upon experiencing the lack of a goal near either cue, participants stopped their searches for the goal in these areas. For this reason, neither males nor females showed preferential exploration of either cue during test, with only a tiny proportion of the 60-second test trial being spent in the vicinity of these cues. It should be noted that this problem is not evident during Experiment 1 as the geometric cues provided during the test trial do not predict the location of the hidden goal nearly so accurately. By using a small goal, placed near, but not coincident with, the corner of a trapezium, a strong search response from participants was elicited. The nature of the cues used for this non-spatial version does not allow for such a perseverative search response.

In order to overcome such an obvious lack of a hidden goal during the test trial, it was decided that the notion of a hidden goal should be replaced with continuous reward for being near certain cues. In this manner, instead of a trial ending once a participant had found the hidden goal, spending time in the location of the goal would allow the participant to accumulate points. Analogous to the hidden goal paradigm, participants gained points displayed on the computer screen for spending time near the compounds of non-geometric cues during training. During the revaluation stage, one of the cues from one compound continued to reward points, whereas one cue from the other compound caused a loss of points. Participants could readily learn the reward contingencies of these cues, as all gains and losses of points were displayed in real-time to them. The crucial difference between the hidden goal and points versions of this task is evident in the test trial. During this trial, by not displaying the gain or loss of points to the participant, but having informed them that they are still gaining, or losing, points for exploring certain cues, a much stronger and more perseverative search response should be elicited. As in Experiment 1, should within-compound associations be present between the cues trained in compound, preferential exploration during the test trial of the cue concurrently trained with the non-revalued cue would be expected. If the inability of females to form within-compound associations in Experiment 1 is a consequence of the apparatus used, then it would be expected that they would fail to demonstrate such associations here. However, if instead the failure is due to a reduced ability to learn about one of the cues trained in compound for females compared with males, then it might be expected, in this non-spatial task, for within-compound associations to be evident in both genders.

4.2.1 Methods

4.2.1.1 Participants

There were 24 participants in this study, eight of whom were male. Ages ranged from 16-26. Males (*M* = 22, *SD* = 2) were significantly older than females (*M* = 19, *SD* = 2), *t*(22) = 3.69, *p* = .001.

4.2.1.2 Apparatus

The virtual environment was created in a similar fashion to that used in Experiment 1. During the training and revaluation stages of the experiment, participants gained points for being in the vicinity of some cues, and lost points when near other cues. The current points total was displayed in the upper-left hand corner of the screen.

The gain and loss of points was displayed clearly to participants on screen as it happened, with their current points updating accordingly. The floors of the arenas in which participants were placed were textured to look like grass, and the view beyond the arena textured to appear as sky. Although no arenas were surrounded by visible walls, invisible barriers prevented participants from falling off the edge of each arena. All training and revaluation trials occurred within a square-shaped arena, with sides 9.6 m in length, across which participants could move at a speed of 1.8 m/s, approximating a brisk walking pace. Participants were able to rotate their view of the arena through 360° in 6 s. Two types of cue were used during this experiment: floating landmarks and coloured areas. The landmark was either a blue cube, with sides of length 32 cm, or a red 3-dimensional star. This star-shaped landmark was 64 cm high and 32 cm wide at its widest point. Both landmarks floated above the floor of the arena at a height coincident with the eye-level of the camera. Each coloured area consisted of three squares, each with sides 96 cm in length, coloured with either a wooden or tiled texture. One of these squares was on the floor of the arena, its pattern simply replacing the grass texture. The other two squares were perpendicular to the floor of the arena, joined to adjacent edges of the first, such that when this coloured area was placed into the corner of the arena, the two upright squares formed a portion of the wall of the arena, intersecting at the corner. The landmark and area cues could be presented in compound, such that the landmark floated within the coloured area. The arena during the test trial was a smaller square, of side length 5.1 m. In each of the corners of this square was an area cue of the same dimensions as during training. Two diagonally opposing corners contained copies of one of the area cues, with copies of the other area cue occupying the remaining two corners. The reason for the smaller arena size during this test trial was so that the identity of the area cues could be clearly differentiated from the participant’s starting position.

4.2.1.3 Procedure

The experiment consisted of eight training trials, four revaluation trials, and a single test trial. A schematic representation of this design can be seen in Figure 4.4.

Participants were instructed that their aim during the experiment was to accumulate as many points as they could. During the training stage, participants were given eight trials in which one of two distinct compounds of landmark and area cues was present. Proximity to these compounds of cues was always rewarded with points. Each compound of cues was presented four times, with the participant beginning each of these four trials at the centre of one of the edges of the arena, facing away from the centre of the arena. Each of the four edges of the arena was used as a starting point once for each compound of cues. The combinations of landmark and area cues were counterbalanced between participants, such that for half of the participants, the cube landmark was paired with the wooden area, and the star landmark with the tiled area, whereas the rest of the participants experienced the cube landmark with the tiled area, and the star landmark with the wooden area. In each trial, participants were given 30 s to accumulate points by spending time in the proximity of the compounds of cues. After this 30 s had elapsed, participants were prevented from moving for 5 s, during which a countdown to the next trial was displayed. In all training trials, there was a compound of cues present that rewarded points. If a participant had not received any points before the 30 s had elapsed, a black column appeared in the centre of the rewarded compound of cues, with an onscreen message instructing participants to navigate to the column, contact with which initiated the countdown for the next trial. Navigating to the column resulted in the participant receiving a small number of points to reinforce that the

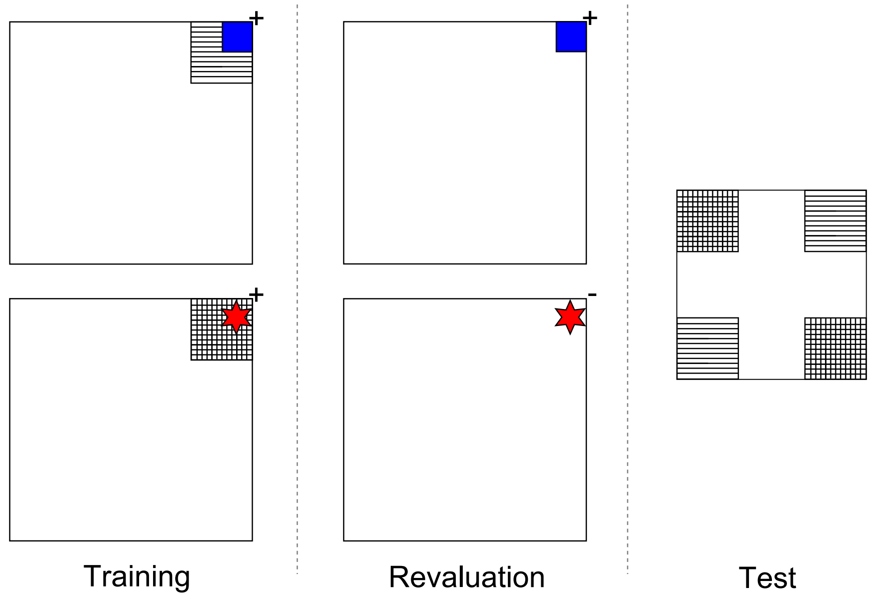


Figure 4.4: A not-to-scale schematic of the design for Experiment 2. The blue square represents the cube-shaped landmark; the star represents the star-shaped landmark; the horizontally-striped square represents the wooden area cue; and the cross-hatched square represents the tiled area cue. Plus (+) signs indicate a cue, or compound of cues, that is rewarded, a minus (-) sign indicates that proximity to the cue will cause a loss of points. Although all stimuli are shown in the top-right corner of the arenas, there were no external cues to provide directional information to participants, who began each trial in different starting locations with respect to the stimuli. In this manner, the position of the stimuli within the environment was unpredictable for the participants.

compound of cues was rewarded. However, this points gain was much lower than if participants had spent time near the rewarded cues during the trial itself. Figure 4.5 provides an example of a participant's view of the arena during a training trial.

During each of the revaluation trials, a single landmark cue was presented without the area cue with which it was paired during training. Spending time in the

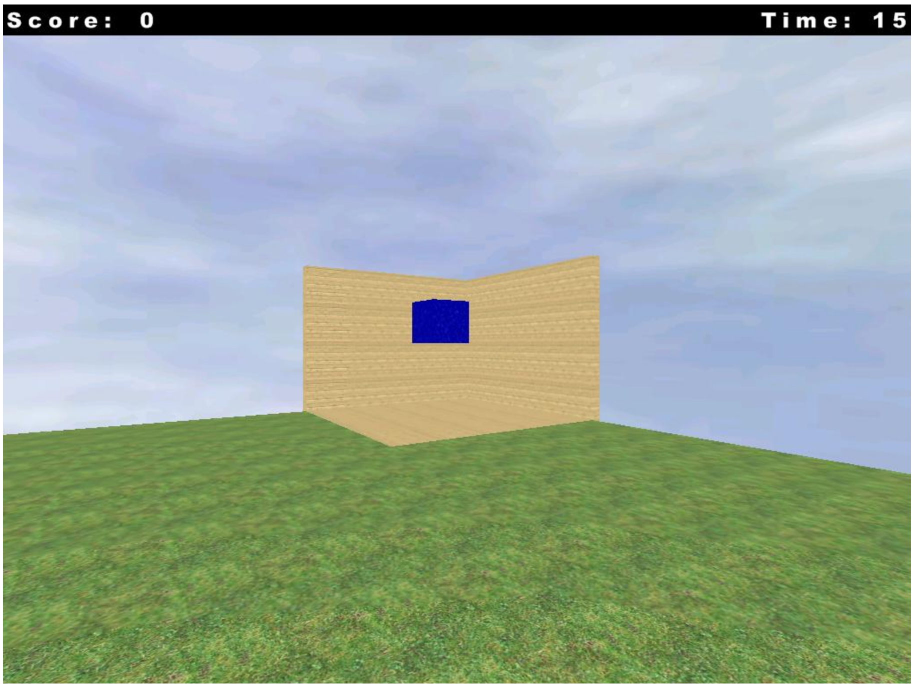


Figure 4.5: The participant's view of the arena during a training trial in Experiment 2.

proximity of one of these landmark cues caused an increase in the participant’s points score, while the other caused a decrease of equal magnitude. Each landmark cue was presented twice during this revaluation stage, with the participant beginning each of the four trials in the centre of one of the four edges of the arena, facing outwards. Each of the four edges was used as a starting point for a single revaluation trial. The identity of the landmark that gave, and hence also the landmark that removed, points was counterbalanced between participants. Each revaluation trial lasted 30 s and the same rules applied as during training for any trials in which a rewarded cue was presented but no points were gained before this time elapsed. The contingency of the first trial was counterbalanced, such that for half of the participants the first trial experienced during this revaluation stage contained a rewarded landmark cue and for the other half of the participants this landmark caused a loss of points.

Participants began the test trial in the centre of the southern-most edge of the arena, facing towards the centre of the arena. They were given 60 s during this test trial to continue to accumulate points. Participants were informed before starting the experiment that points were still being awarded, and they should spend time near those cues they believed would elicit the most points. However, during this test trial the gain and loss of points was not displayed to participants, and the current total points score was hidden. This allowed a demonstration of learning about the area cues in the absence of any feedback. The expectation of points during the final test trial was used as an indication of the amount learned about the two available area cues. This expectation was measured by calculating the amount of time that participants spent exploring within the 96-cm square area cues.

4.2.2 Results and Discussion

4.2.2.1 Training

The amount of time spent by participants in the proximity of the cues present during the training trials can be seen in Figure 4.6. As only four training trials were provided with each compound of cues, and as participants began each of these four trials a varying distance from those cues, it is not possible to accurately compare performance across training trials. For this reason, the data from all four training trials containing the same compound of cues have been combined. These data were split into those trials containing the landmark cue that would be rewarded with points during the revaluation stage, and those that would be revalued, such that they cause a loss of points. This allowed an assurance that both landmark and area cue compounds had been learned about similarly. In this manner, any differences in performance during the test trial could not be attributed to differential learning during the training stage. The data from the training stage showed that there was little difference in time spent in the

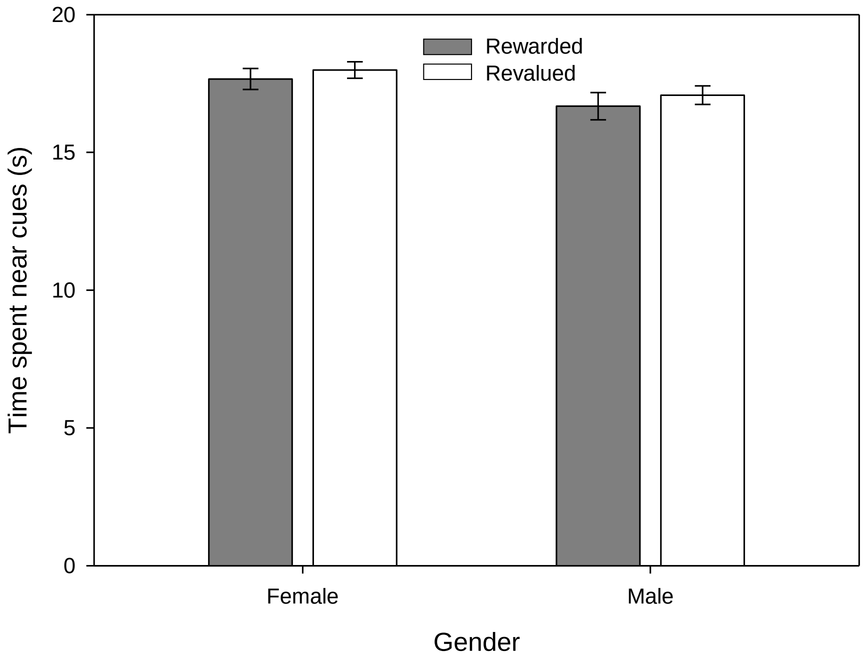


Figure 4.6: Mean time spent in the proximity of cues in the training stage of Experiment 2. The data are split into those trials containing the landmark cue that would be rewarded with points during the revaluation stage, and those that would be revalued, such that they caused a loss of points. Error bars represent ± the Standard Error of the Mean.

proximity of the cues between those trials containing each of the different compounds of landmark and area cues. It is also apparent that there is little difference in the amount of time spent near the cues by males and females.

A mixed model ANOVA (Compound x Gender) confirmed these observations. There was no significant main effect of compound, *F*(1, 22) = 1.36, *p* = .26, and no interaction between compound and gender, *F*(1, 22) = .015, *p* = .91. The main effect of gender approached significance, *F*(1, 22) = 3.94, *p* = .06, with a suggestion that males (*M* = 16.9 s, *SD* = 1.2) spent less time near the cues than females (*M* = 17.8 s, *SD* = 1.4).

It is of no surprise that participants spend a similar amount of time near each compound of cues, during the training stage both cue compounds were rewarded to the same degree. However, it is important that there exists no difference in time spent exploring these different compounds, as it can be inferred from this that they have been learned about similarly. This suggests that any differences during the test trial must be due to the differential effects of the revaluation stage.

4.2.2.2 Revaluation

The amount of time participants spent in the proximity of the available landmark cues during the revaluation stage can be seen in Figure 4.7. There is a clear preference for spending time near the landmark cue that continues to be rewarded with points, compared with the landmark cue that has been revalued and now causes a loss of points. There appears to be little difference between males and females in their discrimination of the two landmarks, both genders spend a similar time near the rewarded landmark and readily avoid the revalued landmark.

These observations are confirmed by a mixed model ANOVA (Landmark x Gender), which shows a significant main effect of landmark, $F(1, 22) = 2230$, $p < .001$, with more time being spent near the rewarded, than the non-rewarded, landmark cue. There was neither a significant main effect of gender nor an interaction between gender and landmark, *F*s < 1.

It was to be expected that participants would spend more time near the rewarded landmark, compared with the revalued landmark, during the revaluation stage, given that participants were informed of all gains and losses to their points score immediately. Participants appeared to have learned very quickly to avoid the landmark cue that caused points to be lost, with only a very small amount of time spent near this landmark. Participants continued to spend a large proportion of their 30-second trial

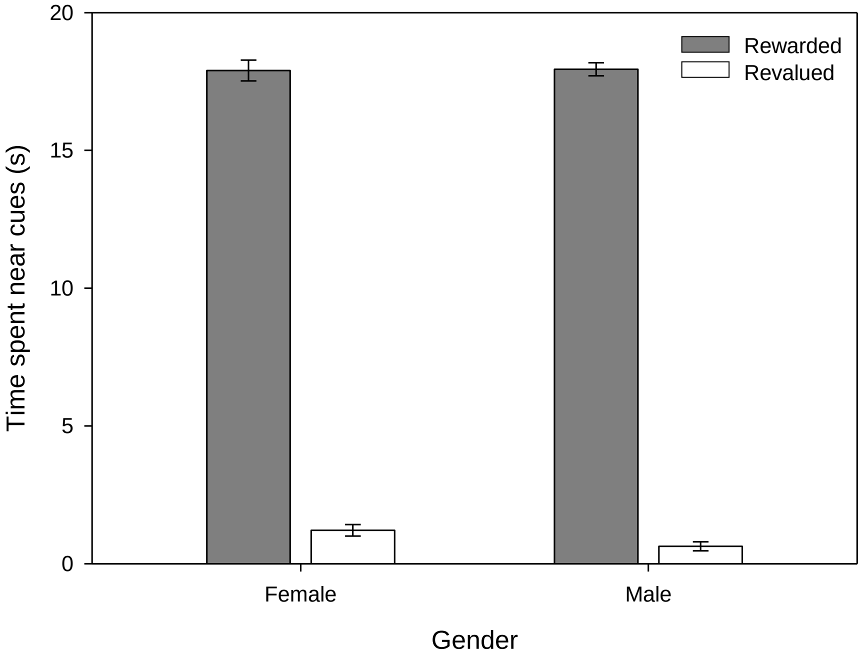


Figure 4.7: Mean time spent in the proximity of the landmark cues during the revaluation stage of Experiment 2. The data are split into those trials containing the landmark cue that continued to be rewarded with points during this stage, and those that had been revalued, such that they now caused a loss of points. Error bars represent ± the Standard Error of the Mean.

time near the rewarded landmark cue, suggesting continued knowledge of its association with the reward. From these data it is clear that that this revaluation stage has succeeded in revaluing one of the landmark cues, which participants learned readily to avoid, and also succeeded in retaining the value of the other landmark cue, near which participants continue to spend time.

4.2.2.3 Test

The time that participants spent in the proximity of the two distinct area cues during the test trial is displayed in Figure 4.8. It can be seen that participants, regardless

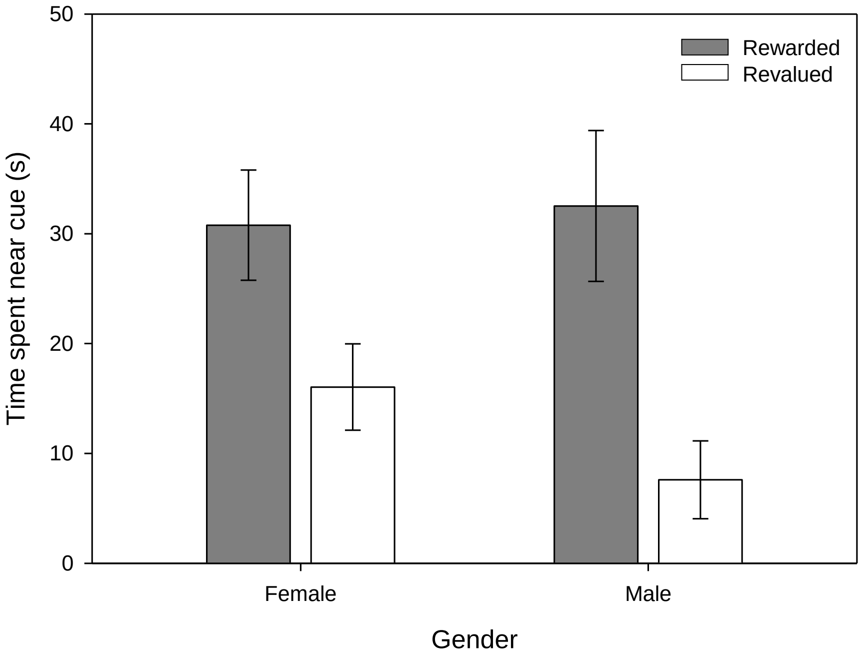


Figure 4.8: Time spent in the proximity of the different area cues during the test trial of Experiment 2. Data are split into rewarded (area cue was paired with the landmark cue that continued to be rewarded during revaluation) and revalued (area cue was paired with the landmark cue that was revalued during revaluation). Error bars represent ± the Standard Error of the Mean.

of their gender, spent more time near those area cues that were initially paired with the landmark that continued to be rewarded during the revaluation stage of training. It is apparent that participants avoided spending time near the area cue associated with the landmark cue that had previously been revalued. This discrimination, although apparent in both genders, appears to be slightly more pronounced for males. A mixed model ANOVA (Cue x Gender) showed a significant main effect of cue, $F(1, 22) = 7.86$, $p = .010$, with significantly more time being spent near the area cue that had previously been paired with the landmark cue that continued to be rewarded during revaluation. There was no significant main effect of gender, $F(1, 22) = 1.93$, $p = .179$, and no significant interaction between cue and gender, *F*(1, 22) = .520, *p* = .479, suggesting that both males and females showed the same preference for the area cue paired with the rewarded landmark.

Data from this test trial support the findings of the experiments from Chapters 2 and 3 in demonstrating the presence of within-compound associations between the cues trained in compound. Despite both area cues having been experienced equally during training and having acquired an equal number of points in the times spent there, participants did not display an equal belief about their relationships with the reward. By revaluing the landmark cue with which an area cue was paired, the area cue underwent revaluation itself. It is reasonable to assume that this occurred via the same mechanism that was argued in favour of in the previous demonstrations of within-compound associations. Sight of one of the area cues during the test trial evoked a representation of the landmark cue with which that area cue had been paired during training. This representation appears to have prevented exploration of the area cue associated with the revalued landmark, in favour of the area cue able to evoke a representation of the landmark cue that was consistently rewarded.

Importantly, this experiment demonstrates that females are able to form within-compound associations between non-spatial cues in a task similar to that of Experiment 1. This would imply that the failure of females to show these associations in the previous experiment is not because of a general failure to associate cues together within this navigational paradigm. Instead, it would seem that the nature of the cues is important in determining whether within-compound associations will form. For females it is apparent that if these cues contain spatial information, in the form of geometric information provided by the shape of the arena, then within-compound associations are unable to form.

4.3 General Discussion

The demonstration of the presence of within-compound associations between spatial and non-spatial cues in humans allows us to assert that the lack of overshadowing in Redhead et al. (2012) is plausibly for the same reason as for similar results in rat studies (e.g., Pearce et al., 2001). During compound training the two cues become associated with one another, as well as with the goal location. Then, during test in the absence of the non-spatial cues, experiencing the spatial cues elicits a representation of the associated non-spatial cue and its relationship with the goal location, counteracting the overshadowing effect that would be predicted by theories of associative learning. Redhead et al. found that this lack of overshadowing only occurred using a triangular arena, and not with a trapezium. Within-compound associations counteracting the effects of overshadowing perfectly explains this difference, as detailed in the introduction to this chapter. In brief, the triangular arena is more salient than the trapezium, and so is overshadowed by the non-spatial cues to a lesser extent. Therefore, the within-compound associations have to compete against a weaker overshadowing effect in the triangular arena, and are able to counteract this overshadowing. However, in the trapezium this overshadowing effect is stronger, due to the lower salience trapezium being more overshadowed by the non-spatial cues, and so the presence of the within-compound associations is not enough to counteract this effect. Whilst Redhead et al. did not find any effect of gender on the levels of overshadowing of geometry by the non-geometric cue, in Experiment 1 within-compound associations were only evident in male participants. This is not a great problem for the within-compound association theory; here it is demonstrated that the presence of within-compound associations between geometric and non-geometric cues is possible in human participants and that it is a potential explanation for the failure to find overshadowing of geometry. Given the differences between the shapes of the arena and the non-geometric cues used between our task and that of Redhead et al., it is more than possible that both males and females were able to form within-compound associations between their cues, whilst our cues prevented the formation of these associations for females.

In Experiment 1 it was shown that human males formed within-compound associations between spatial and non-spatial cues in a virtual environment. Females in this task did not show evidence of the formation of within-compound associations. It was argued that this may be for two reasons: either females cannot form within-compound associations between cues, or the specific nature of the cues used in this experiment did not lend themselves to the formation of these associations for females. In Experiment 2 it was demonstrated that females could form within-compound associations between two non-spatial cues, contradicting the first argument. This suggests that the reason females do not show within-compound associations in Experiment 1 is due to their ability to learn about the spatial and non-spatial cues available. This ability seems to differ between genders, as evidenced by males showing these within-compound associations. It might be predicted, therefore, that females are unable, or much less able than males, to utilize one of the two available cues to learn the location of the goal during compound training. No learning to one of the compound of cues would obviously result in an inability to form a within-compound association between the cues of that compound. On the other hand, reduced learning to one of the cues would not prohibit the formation of within-compound associations between those cues. However, it would mean that the presence of these within-compound associations would have a lesser effect on performance. Given the evidence of within-compound associations between two non-spatial cues in Experiment 2, it seems unlikely that females were unable to learn about the non-spatial cues in Experiment 1. However, neither the reward afforded by learning about the cues, nor the cues themselves, were equivalent between these experiments, and so the possibility should be entertained that females were unable to learn about the non-spatial cues in Experiment 1. Therefore, if it is assumed that the poorly learned cue is the non-spatial cue (the cue to undergo revaluation), then it should be obvious that the revaluation stage should be much less successful for females than for males, as the cue to be revalued is differently salient to each gender. Although the data show that males and females did not differ in their time taken to locate the goal during the rewarded revaluation trials, it is impossible to say whether the two genders underwent equivalent extinction of the non-spatial cue presented in the absence of the goal. If this non-spatial cue was learned about less readily by females than by males, it is no great stretch to expect this revaluation stage to have been less effective for females. This would lead to poorer discrimination between the spatial cues presented during the test trial, as can be seen from the female data. Alternatively, the more plausible scenario is that females were unable to learn about the spatial cues in Experiment 1. If this were the case, then during training with the compound of cues very little would be learned about these spatial cues. Whilst revaluation of the non-spatial cue may proceed to the same degree as for males, something to which the revaluation data hint, the discrimination of the spatial cues during test would be poor, given that relatively little had been learned about these cues.

Given the presence of within-compound associations between non-spatial cues for both males and females, but the absence of these associations between spatial and non-spatial cues in females, it seems apparent that the spatial and non-spatial cues used in Experiment 1 have been learned about differently depending on gender. Chapter 5 will build upon these ideas and further explore the abilities of males and females to learn about similar spatial and non-spatial cues.

CHAPTER FIVE

Gender Differences in Geometry Learning

The experiments presented in Chapter 4 suggested that human males were able to form within-compound associations between spatial and non-spatial cues in a 3-dimensional virtual environment. However, females did not show any evidence of within-compound associations between these cues, despite readily showing within-compound associations between two non-spatial cues. The argument was made that this difference in the ability to demonstrate the presence of within-compound associations between males and females implied that learning about the cues to be associated together was not equivalent between genders.

There exists a reliable difference between the performances of males and females in spatial ability (Linn & Petersen, 1985; Voyer, Voyer, & Bryden, 1995). Adult human males have been shown to perform better than females on pencil-and-paper tasks such as route learning (e.g., Dabbs, Chang, Strong, & Milun, 1998; Galea & Kimura, 1993), and mental rotation (e.g., Dabbs et al., 1998; Linn & Petersen, 1985). Despite these findings, the differences between pencil-and-paper tasks and real-world navigation, discussed at length in Chapter 4, could mean that these established gender differences do not accurately represent differences in navigation in other tasks. However, gender differences have also been demonstrated extensively in virtual environments with both adult humans (e.g., Astur et al., 1998; Astur et al., 2004; Cutmore, Hine, Maberly, Langford, & Hawgood, 2000; Moffat, Hampson, &

Hatzipantelis, 1998; Mueller, Jackson, & Skelton, 2008; Sandstrom et al., 1998) and children (e.g., Jansen-Osmann & Wiedenbauer, 2004; Newhouse, Newhouse, & Astur, 2007). Furthermore, these differences in spatial ability between males and females are not confined to humans, and have been found in deer mice (Kavaliers, Ossenkopp, Prato, Innes, Galea, & Kinsella, 1996), mice (Mishima, Higashintani, Teraoka, & Yoshioka, 1986), meadow voles (Gaulin & Fitzgerald, 1986; Gaulin & Fitzgerald 1989; Kavaliers, Ossenkopp, Galea, & Kolb, 1998), rats (Cimadevilla et al., 1999; Dawson, 1972; Einon, 1980; Faraji, Metz, & Sutherland, 2010; Rodriguez, Torres, Mackintosh, & Chamizo, 2010; Seymoure, Dou, & Juraska, 1996), and rhesus monkeys (Lacreuse, Herndon, Killiany, Rosene, & Moss, 1999). This pervasion of a sex difference in spatial ability throughout a variety of tasks in a diverse range of species supports the assertion of a difference between males and females in their abilities to make use of the available cues in Experiment 1 of Chapter 4.

During the compound training stage of Chapter 4 Experiment 1, participants were required to use both the landmark and the geometry cues to learn to locate the hidden goal accurately. Given their ability to show within-compound associations between non-spatial cues it seems unlikely that the reason for the failure of females to show these associations between a spatial and a non-spatial cue is due to a lack of learning about the non-spatial cue. Instead, a much more plausible argument as to why females did not show within-compound associations is because of their reduced preference for learning about geometric cues when compared with males. That males more readily learn about, and make use of, geometric cues within a spatial task is well reported in rats (e.g., Rodriguez, Chamizo, & Mackintosh, 2011), human children (e.g., Lourenco, Addy, Huttenlocker, & Fabian, 2011), and human adults (e.g., Lövdén, Herlitz, Schellenbach, Grossman-Hutter, Krüger, & Lindenberger, 2007). Therefore, it would be unsurprising if there was a difference in how well males and females learned about the geometric cues present during this compound training stage, with reduced learning from females being the cause of their inability to discriminate between the geometric cues presented in conflict during the test trial.

It is therefore apparent that males and females differ in the extent to which they rely upon different types of cue. There is some evidence that males rely more on geometric cues, whereas females rely more on landmark cues. The effect of this difference in reliance on learning about these cue types will be further investigated in this chapter. Experiment 1 attempted to show a difference in the ability of males and females to learn about geometry and landmark cues when presented in compound. Experiments 2A and 2B attempted to resolve a confound from Experiment 1, to demonstrate that the difference in learning evident in Experiment 1 was not the result of a gender-difference in strategy-switching ability. Experiment 3 further demonstrated males' superior geometry performance using a more direct test of learning. This superiority of geometry learning can readily explain the failure to witness within-compound associations in females in Experiment 1 of Chapter 4.

5.1 Experiment 1

A difference in the abilities of males and females to learn about the relevance of geometric cues may explain the gender difference evident in Chapter 4 Experiment 1. Sandstrom et al. (1998) provided a demonstration of such a difference by training participants to locate a hidden goal in a virtual MWM. Initially, both distal landmark cues and the shape of the room were available for learning the location of the hidden goal. After six trials of compound training, both males and females were locating the goal at asymptotic performance, with no differences between the genders during training. Two manipulations then revealed a clear gender difference. When the landmarks were either removed completely, or moved randomly such that they no longer predicted the location of the hidden goal, females required much more time to locate the platform than males. These manipulations left only the geometric cues provided by the shape of the room available for locating the goal. This would suggest that during the compound training, males had learned more about the relevance of the geometric cues than females, and as such were able to locate the hidden goal more rapidly when only geometric cues indicated its location. A further manipulation, in which the geometric cues were removed, but the landmark cues remained, demonstrated no such difference between males and females, suggesting that learning about the relevance of landmark cues for locating the goal was similar between the genders. Importantly, there was very little difference in the times taken to find the goal before and after the removal of the geometric cues. This suggests that using the landmarks to locate the hidden goal had been the preferred method for both genders during compound training.

There are several crucial differences between the cues used in Sandstrom et al.'s (1998) study and those in Experiment 1 of Chapter 4, in which a similar gender difference is also demonstrated. Firstly, Sandstrom et al. used distal landmark cues positioned outside of the arena, whereas the landmark cues used in Chapter 4 Experiment 1 were proximal, positioned within the bounds of the area in which the participants could manoeuvre. Additionally, their geometric cues were provided by the shape of the room that surrounded the arena, whereas it was the shape of the arena itself that acted as the geometric cues in the previous chapter. Therefore, in order to extend the generality of Sandstrom et al.'s assertions, and to assess whether an explanation based on differential geometry learning could explain the gender differences found in the previous chapter, a replication of Sandstrom et al.'s results is required, using apparatus much more similar to that used in Experiment 1 of Chapter 4.

Participants were initially trained to locate a hidden goal with respect to a compound of landmark and geometry cues. The landmark cues were then moved and rotated around the arena between trials, with the hidden goal remaining stable with respect to only the geometry cues. Although Sandstrom et al. (1998) conducted two manipulations in which only geometric cues remained reliable indicators of the platform's position, this experiment involved only a single manipulation following compound training. In Sandstrom et al.'s task, randomly moving the landmarks produced a greater deficit to performance for both males and females than removing the landmarks completely. Therefore, in an attempt to avoid making the task too easy and failing to see a difference in geometry learning, this more difficult manipulation was employed in this experiment. A gender difference in geometry learning would be evidenced by a comparison of any difference between genders at the end of compound training with any difference between genders following the movement of landmark cues. If both genders find the hidden goal equally well following compound training, then superior geometry learning for males would manifest as a shorter time required to find the platform, compared with females, following the landmark manipulation.

5.1.1 Method

5.1.1.1 Participants

Twenty participants took part in this experiment, with equal numbers of males and females. The ages of participants ranged from 19-28, with no significant difference between the ages of males (*M* = 22, *SD* = 3) and females (*M* = 20, *SD* = 1), *t*(18) = 1.21, *p* = .24.

5.1.1.2 Apparatus

A custom-built 3D virtual environment (VE) was created for this experiment that was presented to participants in the same manner as during Chapter 4. The arenas for this experiment were all trapezium-shaped and were identical to the trapezium-shaped arena used in Chapter 4. Movement and rotation speed were identical to those described previously.

In all trials, a square-shaped hidden goal, with side length 64 cm, was located to the right-hand side of the short parallel wall. The current trial was ended once a participant had made contact with this hidden goal location. Four landmarks were also visible in the arena: a green cone (40 cm diameter x 64 cm height), a purple hexagonal prism (75 cm width x 32 cm height), a yellow cuboid (48 x 48 x 56 cm height) and a red sphere (64 cm diameter). In all stages of the experiment, these landmarks were arranged in a configuration such that if a line were drawn around the array, a square would be formed. Landmarks were located 2.7 m away from their closest neighbours. During Stage 1, the position of these landmarks remained constant, with the centre of the landmark array coinciding with the centre of the trapezium. The green cone was closest to the shorter of the two parallel walls, with the purple prism, yellow cuboid, and red sphere occupying positions at 90, 180, and 270°, respectively. The position of this landmark array changed in Stage 2 of training, during which the location and orientation of the landmark array varied in a pre-determined, but essentially random, manner with respect to the shape of the arena between trials.

5.1.1.3 Procedure

All participants completed 16 trials in which they were given 120 s to locate a hidden goal. On each trial, participants started from the midpoint of one of the four walls, facing inwards towards the centre of the arena. Each of the four walls of the trapezium was used as a starting location once per block of four trials, with starting locations pre-determined to appear random. Starting locations were different for all blocks of four trials, and no single starting location was used in successive trials. A trial ended when the participant moved over the hidden goal, at which point they were notified on screen. Once a trial was ended, translational motion was prevented, but rotational motion was preserved for ten seconds to allow participants to familiarise themselves with the position of this hidden goal. If participants did not find the goal within 120 s, it became visible and participants had to move over it to end the trial, at which point the same ten-second procedure as before was initiated. In all trials, latency to locate the position of the hidden goal was recorded.

Compound training consisted of two blocks of four trials. Participants were placed into the trapezium arena with landmarks present. Both the landmarks and geometry of the arena provided stable indications as to the location of the hidden goal. During geometry training, which also consisted of two blocks of four trials, the

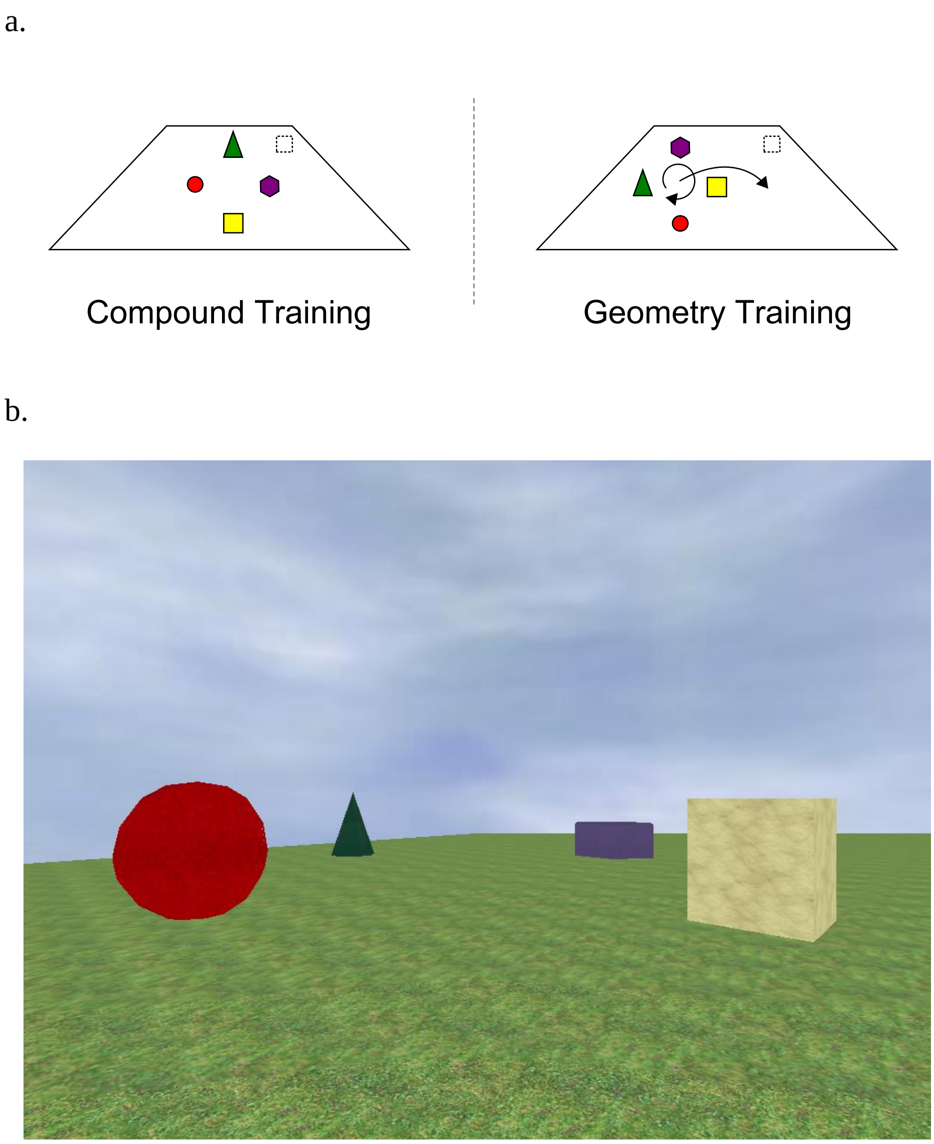


Figure 5.1: A not-to-scale schematic of the design of Experiment 1 (a) and a participant's view of the arena during compound training (b). The dashed square represents the location of the hidden goal. The array of landmark cues remained static during compound training, but was rotated and translated between trials during geometry training such that the landmarks became unreliable for locating the goal.

geometry remained a reliable indicator of the hidden goal’s location, but the location and orientation of the landmark array varied in a pseudorandom fashion with respect to the shape of the arena. The landmark array therefore became an unreliable cue for locating the hidden goal. A schematic of the procedure for this experiment and a participant's view during compound training can be seen in Figure 5.1.

5.1.2 Results and Discussion

The time taken for males and females to find the hidden goal during both compound and geometry training stages can be seen in Figure 5.2. Over the course of compound training both males and females reduced the amount of time required to locate the goal such that by the end of compound training there was little difference between the genders. However, at the start of geometry training a large difference

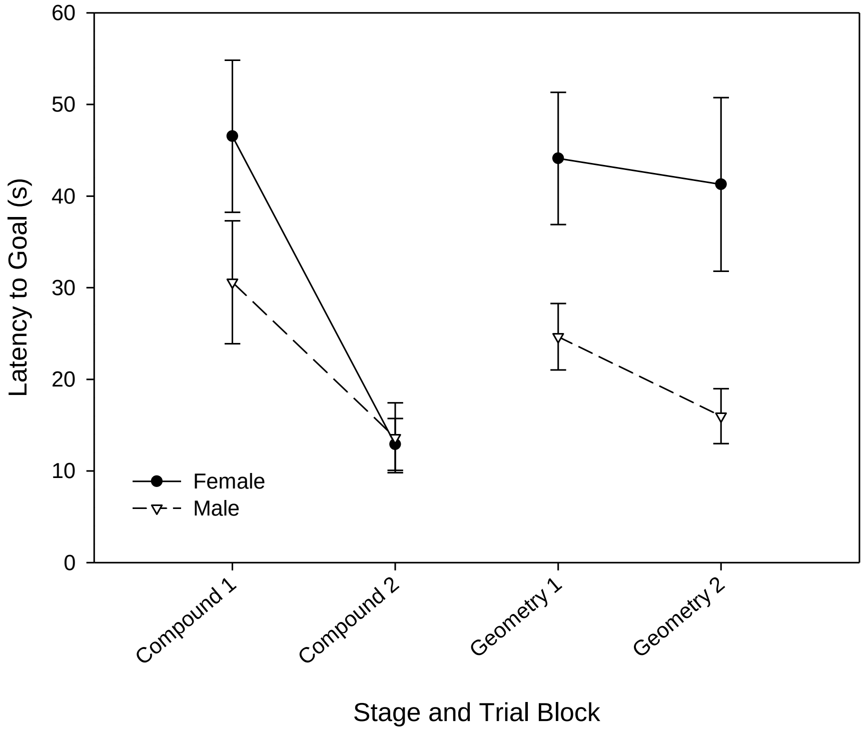


Figure 5.2: The time taken for participants to locate the hidden goal during compound and geometry training stages in Experiment 1, split by gender. Each data point represents the average of four successive trials, to equate for distance to the hidden goal from the starting location.

appeared between males and females, with females requiring much more time to locate the hidden goal than males. Over the course of geometry training this difference remained evident, with females showing little improvement in their time taken to find the goal.

In order to determine the extent to which the change in reliability of landmark cues affected the time taken to find the hidden goal, a mixed model ANOVA (Gender x Stage) was conducted on the mean time to find the goal for males and females for the final four trials of compound training and the initial four trials of geometry training. Importantly, there was a significant interaction between gender and stage, $F(1, 18) = 5.20$, $p = .035$. Analysis of the simple main effects of this interaction showed that whilst there was no difference between genders in the time taken to find the goal at the end of compound training, $F(1, 18) = .023$, $p = .88$, females took significantly longer than males to find the hidden goal at the start of geometry training, $F(1, 18) = 5.80$, $p = .027$. Additionally, females took significantly longer to find the hidden goal at the start of geometry training than they had taken at the end of compound training, $F(1, 18) = 24.86$, $p < .001$. However, there was no such increase in the time taken to find the hidden goal for males, $F(1, 18) = 3.10$, $p = .095$. In addition, there was a significant main effect of stage, $F(1, 18) = 22.8$, $p < .001$, with participants requiring considerably more time to locate the hidden goal at the outset of geometry training when compared with the end of compound training. The main effect of gender approached significance, $F(1, 18) = 3.62$, $p = .073$, with a suggestion that males were quicker to find the hidden goal than females, regardless of the stage of the experiment.

These data suggest that males and females were differentially affected by the landmark cues becoming irrelevant for locating the hidden goal. Despite both genders showing similar competence at locating the goal after compound training, only females were significantly disrupted by the landmark manipulation. This finding appears to support the claim that males learn more about geometric cues than females when trained with landmarks and geometry in compound. However, there is a confound present in this study, which is also present in the study by Sandstrom et al. (1998), that allows another explanation for males not being as affected by the movement of the landmark cues as females. It has been argued that a difference in the ability of males and females to switch the strategy they use to locate the hidden goal could be responsible for such gender differences.

Studies of this ability to switch strategies have tended to demonstrate that males possess a more flexible approach to strategy use (Cazzato, Basso, Cutini, & Bisiacchi, 2010; Sandstrom et al., 1998). A study by Kelly and Bischof (2005) presented a clear illustration of how gender differences in spatial learning can be the consequence of either differences in geometry learning or strategy switching. They trained human participants initially to locate a hidden goal with reference to both landmark and geometric cues in a virtual environment. Following such training, the landmark cues were removed. Whilst males were able to locate the goal even without these landmark cues, females failed to do so. One explanation for this result is that males had learned more about the relationship between the geometric cues and the hidden goal during compound training than had females. Therefore, during the training in which the landmarks were removed, males could rely on their previous learning about the geometric cues to locate the goal. Females, having learned less about the relationship between geometry and the hidden goal during compound training, were unable to locate the goal based solely on the remaining geometric cues. Alternatively, the gender difference could be a result of males being able to switch the strategy they were using to find the hidden goal much more quickly than females once the landmark cues had been removed. Unless the geometric cues were vastly more salient than the landmark cues, it is likely that both males and females were using landmark cues to some extent to locate the hidden goal. When these landmark cues were removed, males could have switched to locating the goal solely based on geometric cues more quickly than females. Males and females may well have learned a similar amount about both landmarks and geometry during training, with the gender difference being determined only by the speed at which they could switch to a strategy involving only geometric information.

During compound training, the location of the hidden goal can be learned not only by reference to the landmark cues present, but also by using the geometric cues provided by the shape of the arena in this experiment, or the shape of the room in Sandstrom et al. (1998). Therefore, a difference in their ability to switch strategies can only explain the difference between males and females in these experiments if we assume that the amount learned about the relationship between the geometric cues and the hidden goal was similar between genders. If, on the other hand, we do not assume similar geometry learning, and instead suggest that males learned more about the geometry cues during compound training than did females, then there need be no such difference in ability to switch from a landmark-based to a geometry-based strategy. Males would simply have learned more about the relationship between geometric cues and the hidden goal during the compound training, and so when presented with only the geometric cues relevant during geometry training would have been at less of a disadvantage for locating the hidden goal compared with females, who had learned less about the geometry-goal relationship. Despite the previously discussed studies showing superior geometry learning by males, the evidence for this gender difference is far from unequivocal, especially in human studies. Redhead and Hamilton (2009) and Wilson and Alexander (2010) both report no gender differences in a variety of blocking experiments involving the interaction of landmark and geometry cues. It would therefore appear that gender differences in learning about geometry cues are dependent on the conditions under which learning is required to progress. Therefore, it is necessary to examine, under conditions as similar to Experiment 1 as possible, whether a gender difference in geometry learning, or in strategy-switching, is responsible for the observed superiority of male participants.

In order to determine whether the gender difference apparent in Experiment 1 is a consequence of differential geometry learning, it can be assessed whether a similar gender difference exists under conditions in which differential geometry learning cannot take place. This would allow us to assess directly the abilities of males and females to switch between a landmark-based and a geometry-based strategy, and whether a gender difference exists for this strategy-switching. In order to remove potentially confounding geometry learning, initial landmark training must take place in the absence of relevant geometric cues. If, having removed these geometric cues, a difference between males and females remains, then the theory that males are more readily able to switch strategy than females would gain support. On the other hand, if the removal of relevant geometric cues also removes any gender difference then a difference in strategy-switching ability between males and females is called into question, and the extent of geometry learning during initial compound training would need to be further explored.

5.2 Experiment 2A

In order to assess the effect of a direct switch of strategy, from landmark-based to geometry-based, on the ability of males and females to locate a hidden goal, Experiment 2A was a repetition of Experiment 1 but without the confound of relevant geometric cues during compound training. During the first stage of training, the landmarks moved around the arena as they had done during geometry training in Experiment 1. However, rather than the hidden goal remaining static with respect to the geometric cues, it retained its spatial relationship with the landmark array, moving around the arena in concert with the landmarks. This had the effect of rendering the shape of the arena unreliable for locating the hidden goal, whilst the landmarks reliably predicted the goal's location. The second stage of training then proceeded in exactly the same manner as the geometry training stage of Experiment 1. This design allowed it to be determined if there was a difference between males and females in their abilities to switch from a landmark-based to a geometry-based strategy. The transition between the landmark training and geometry training stages of this experiment required a strategy switch. As such, if males and females were similarly impaired by this transition, then that would suggest that there was no difference in their abilities to switch strategy. Conversely, it is conceivable that the results of Experiment 1 are due to females switching strategy less readily than males. Support for this theory would be provided by females showing a greater impairment than males by the transition from a landmark-based to a geometry-based strategy in this experiment.

5.2.1 Method

5.2.1.1 Participants

Twenty people participated in this experiment, half of whom were male. The age range of participants was 17-38, and there was no difference in the mean age of males (M = 20, SD = 1) and females (M = 23, SD = 5), $t(18) = 1.59$, $p = .13$.

5.2.1.2 Apparatus

The apparatus used for this experiment was essentially the same as that used in Experiment 1. During both landmark and geometry training stages, the landmark array was rotated and translated within the arena. During landmark training, the location of the hidden goal remained constant with respect to the landmark array. The distance and direction of the goal from the centre of the landmark array were the same as during compound training in Experiment 1. During geometry training, the hidden goal was located in the same position as during compound training of Experiment 1, with its relationship to the landmark array changing as the position of the array changed between trials.

5.2.1.3 Procedure

The procedural design for this experiment can be seen in Figure 5.3. Participants were initially given eight trials of landmark training, during which the landmark array and hidden goal moved around the arena in concert. Therefore, only the landmarks could be use to locate the goal, as the goal's position was ever-changing with respect to the shape of the arena. This was followed by 16 trials of geometry training, during which the landmark array continued to move, but the hidden goal remained in a stable location with respect to the shape of the arena. All other procedural details remained

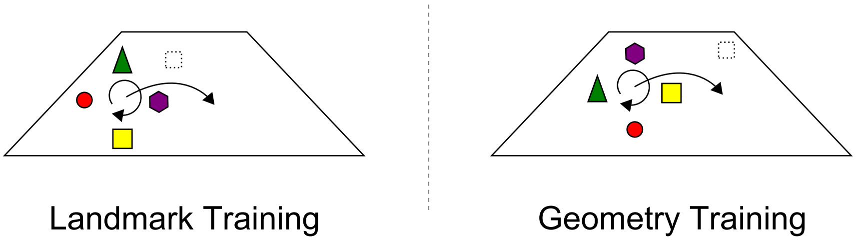


Figure 5.3: A not-to-scale schematic of the design of Experiment 2A. The dashed square represents the location of the hidden goal. The array of landmark cues is rotated and translated between trials during both stages of training.

identical to those used in Experiment 1.

5.2.2 Results and Discussion

The times required for both males and females to locate the hidden goal during landmark and geometry training can be seen in Figure 5.4. Over the course of both stages of training males took less time to locate the goal than females. Both genders appear to have taken less time to locate the goal as training in each stage progressed, with a pronounced increase in latency between the end of landmark training and the beginning of geometry training. The rate at which latencies decreased within each stage of training, and hence the rate of learning, was similar between males and females.

As in Experiment 1, a mixed model ANOVA (Stage x Gender) was conducted on the time taken to locate the hidden goal for the final four trials of the first stage of training and the initial four trials of the second stage of training. There was a significant main effect of stage, $F(1, 18) = 150$, $p < .001$, with participants taking longer to find the hidden goal during the first four trials of geometry training than during the last four trials of landmark training. There was also a significant main effect of gender, $F(1, 18) = 11.7$, $p = .003$, suggesting that males took less time to find the hidden goal

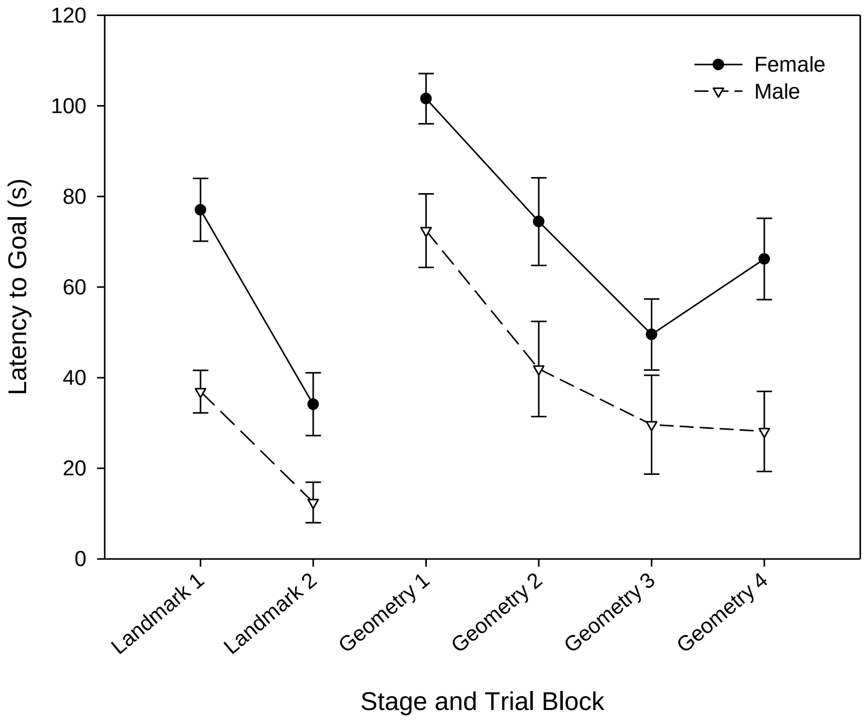


Figure 5.4: The time taken for participants to locate the hidden goal during landmark and geometry training stages in Experiment 2A, split by gender. Each data point represents the average of four successive trials, to equate for distance to the hidden goal from the starting location.

than females overall. However, in contrast to Experiment 1, there was no interaction between stage and gender, *F*(1, 18) = .51, *p* = .48, indicating that both males and females suffered a comparable increase in time taken to locate the goal as a result of the change from landmark training to geometry training.

Both males and females suffered a significant decrease in time taken to find the hidden goal upon transition from landmark training, in which only the landmarks could be used to locate the goal, to geometry training, in which only the geometry of the arena could be used to locate the hidden goal. However, unlike in Experiment 1, this decrease in performance accompanying the change in cues that indicated the location of the hidden goal appears to have affected both males and females to the same degree. The data from this experiment suggest that when participants were required to make a strategy switch, from locating a hidden goal with respect to landmark cues to locating that goal with respect to geometric cues, there was no difference in the effect on performance this had between males and females. Comparing these data with those of Experiment 1, it would appear that the absence of reliable geometry cues during the first stage of training results in males being as much affected by the transition to geometry training as females. However, it could be argued that a difference in strategy-switching ability between the genders may be difficult to observe in the first few trials following a change in cue-contingencies given that it would take a few trials for participants to learn that there is a new strategy to which they must switch. It might be thought that any difference in strategy-switching ability would manifest as the second stage of training progresses, with those participants able to switch strategy more readily showing a more rapid rate of learning during this second stage. In order to address this concern, a mixed model ANOVA (TrialBlock x Gender) was conducted on the time taken to locate the hidden goal during the geometry training stage. There was a significant main effect of trialBlock, $F(3, 54) = 18.7$, $p < .001$, with time taken to find the goal decreasing with increased training. There was also a significant main effect of gender, $F(1, 18) = 9.89$, $p = .006$, with males taking less time to locate the goal than females. Importantly, there was no interaction between these two main effects, $F(3, 54) = .63$, $p = .60$. This lack of an interaction would suggest that the rate of learning about the location of the hidden goal with respect to the geometry cues in this second stage of training does not differ between males and females. Therefore, there appears to be no difference in their strategy-switching ability even when the entire second stage of training is accounted for. This goes counter to an argument put forward by Sandstrom et al. (1998) that the male superiority displayed in Experiment 1 is due to their ability to change from a landmark-based to a geometry-based strategy more quickly. This would suggest that, in Experiment 1, the difference in performance between males and females during the geometry training was a consequence of differential learning about geometric cues during compound training. Had males learned more about geometric cues when trained with a compound of landmark and geometry than females, then this learning could have improved their performance during the geometry training stage. A demonstration of superior geometry learning by males after compound training with both landmarks and geometry, in exactly the same manner as Experiment 1, would strengthen this argument.

However, before an attempt to show better geometry learning in males than in females during compound training, an alternative explanation for the results of this experiment should be addressed. It is possible that the lack of an apparent difference between males and females in their ability to switch strategy from landmark to geometry learning is due to differential learning about the irrelevance of geometry during landmark training. In this experiment, landmarks were not trained on their own, but in concert with irrelevant geometric cues, which were unreliable for locating the hidden goal. If geometric cues are more salient for males than for females, then it would be expected that, during landmark training, males would learn more about the irrelevance of the geometric cues than females. This would serve to reduce the rate at which males could learn about the relevant geometric cues during geometry training, through latent inhibition (Lubow & Moore, 1959). As females would learn less about the irrelevance of the geometric cues during landmark training, they would not display such a reduced rate of learning towards those cues during geometry training. Without this latent inhibition, we might expect males to locate the hidden goal with respect to geometric cues much more quickly than they did, and an ability to switch strategies more readily than females may have been evident. Therefore, to counter this argument, the same lack of a difference between males and females in their ability to switch strategies should be evidenced in a similar study that does not suffer from the confound of irrelevant geometric cues during the landmark training stage. If this can be shown, then it would strongly suggest that switching from a landmark-based to a geometry-based strategy occurs equally well in males and females. In addition, it would also imply that the results of Experiment 1 are explicable in terms of differential geometry learning during compound training.

5.3 Experiment 2B

Experiment 2A suffered from the confound of irrelevant geometric cues being present during landmark training. Differential learning about the irrelevance of these cues could have inhibited subsequent geometry learning differently for males and females. A more convincing demonstration that males and females are able to switch strategies equally well would remove the confounding geometric cues during landmark training, and instead train participants to locate the hidden goal with only landmark cues present. It is simple to present landmark cues within an arena that provides irrelevant geometric information, for example in a square or circular arena. However, despite participants being unable to learn the irrelevance of the trapezium-shape for locating the hidden goal, the irrelevance of geometric cues in general could still be learned. Therefore, there would remain the problem that the irrelevance of this geometric information may not be equally learned by both genders. One solution to this problem is to provide an environment to participants that contains no geometric information; that is, it extends indefinitely in all directions, with no visible boundaries save for the virtual horizon. However, this presents some practical problems, namely that the environment can only extend as far as the software allows, and that participants could continue to navigate away from the landmark cues indefinitely. In Experiment 2B, these problems were overcome by having the arena floor extend as far as the participants could see, with an invisible boundary keeping participants within the vicinity of the landmarks. This invisible boundary was circular, with its centre coincident with the centre of the landmark array. With this arrangement, participants could learn only about landmark cues during the landmark training; there were neither relevant nor irrelevant geometry cues available. Obtaining the same results as Experiment 2A would strongly suggest that both males and females switch from a landmark-based to a geometry-based strategy equally well, suggesting that the gender differences shown in Experiment 1 were a result of differential geometry learning during compound training.

5.3.1 Method

5.3.1.1 Participants

There were twenty participants in this experiment, with equal numbers of males and females. The age range was 18-24, and there was no significant difference between the ages of males (*M* = 21, *SD* = 1) and females (*M* = 20, *SD* = 2), *t*(18) = .15, *p* = .88.

5.3.1.2 Apparatus

The floor of the arena during landmark training extended as far as was visible to participants. This resulted in there being no discernible geometric cues available for participants to use for locating the position of the hidden goal. An array of landmarks, identical to those used during compound training in Experiment 1, was present in the centre of the arena. An invisible circular barrier with a radius of 7.7 m, the centre of which coincided with the centre of the landmark array, prevented participants from navigating too far away from these landmark cues. The hidden goal was identical in size and location with respect to the landmark array as during the compound training in Experiment 1. Geometry training progressed in exactly the same manner as the geometry training stages in both Experiments 1 and 2A.

5.3.1.3 Procedure

The design of Experiment 2B can be seen in Figure 5.5. Participants were initially trained, over eight trials, to locate a hidden goal with respect to the same landmarks as in the compound training stage of Experiment 1. Here, however, the

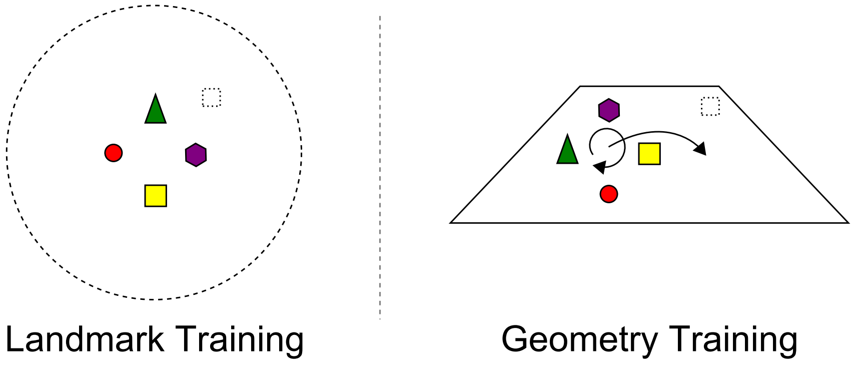


Figure 5.5: A not-to-scale schematic of the design of Experiment 2B. The dashed square represents the location of the hidden goal. The large dashed circle represents the invisible boundary present during landmark training, beyond which the arena continued indefinitely. During geometry training, the array of landmark cues is rotated and translated between trials.

landmarks were present within an arena with no visible boundaries. The ground extended as far as could be seen in all directions and participants were kept in the vicinity of the landmarks by an invisible circular barrier. The location of the hidden goal could therefore be learned with respect only to the landmark cues provided. The distance and direction from the landmark array to the hidden goal was identical to that used during compound training of Experiment 1. Participants were then given the same training as in the geometry training stage of Experiment 2A.

5.3.2 Results and Discussion

The times required for both males and females to locate the hidden goal during landmark and geometry training can be seen in Figure 5.6. The data very closely resemble those of Experiment 2A, with males showing lower latencies to find the hidden goal than females. Again, both genders took less time to locate the goal as training progressed, with this improvement in performance being similar between

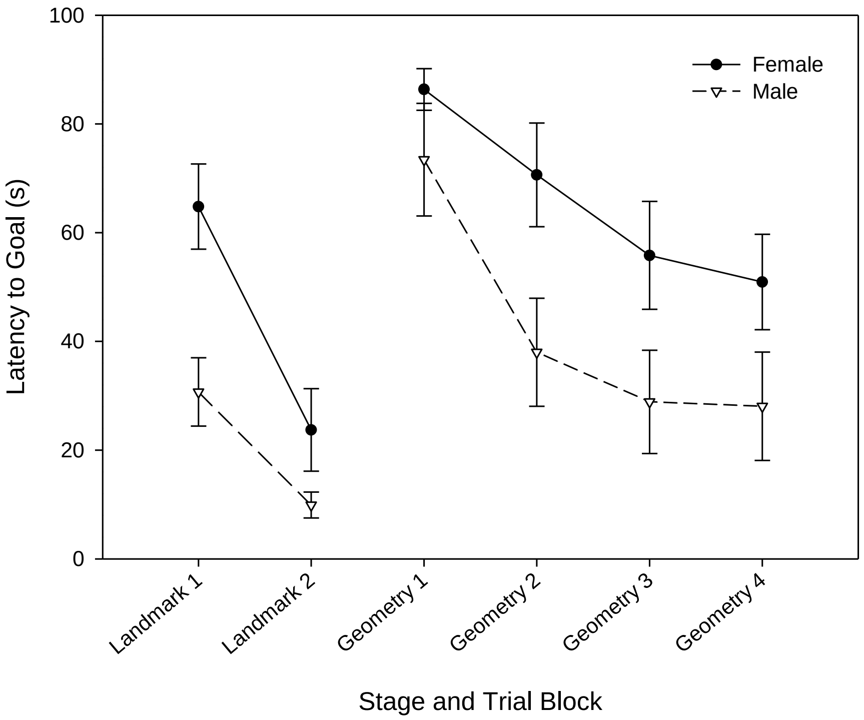


Figure 5.6: The time taken for participants to locate the hidden goal during landmark and geometry training stages in Experiment 2B, split by gender. Each data point represents the average of four successive trials, to equate for distance to the hidden goal from the starting location.

genders. A pronounced increase in latency occurred between the end of landmark training and the beginning of geometry training, as in Experiment 2A.

As in Experiment 2A, a mixed model ANOVA (Stage x Gender) was conducted on the average time taken to find the hidden goal during the final four trials of landmark training and the initial four trials of geometry training. There was a significant main effect of stage, *F*(1, 18) = 94.1, *p* = .001, with participants taking significantly longer to find the hidden goal at the start of geometry training than at the end of landmark training. The main effect of gender approached significance, *F*(1, 18) = 3.56, *p* = .076, with males taking less time to locate the hidden goal than females overall. There was no significant interaction between stage and gender, $F(1, 18) = 0.01$, $p = .95$, suggesting that the transition from landmark to geometry training affected the time taken to find the hidden goal similarly for both males and females.

As in Experiment 2A, a mixed model ANOVA (TrialBlock x Gender) was conducted on the time taken to locate the hidden goal during the second stage of training, to counter the argument that any difference in strategy-switching ability may not manifest within the first few trials of this second stage. There was a significant main effect of trialBlock, $F(3, 54) = 16.7$, $p < .001$, with time taken to find the goal decreasing as the second stage of training progressed. There was also a significant main effect of gender, $F(1, 18) = 5.24$, $p = .034$, with males finding the goal more quickly than females. There was no interaction between trialBlock and gender, $F(3, 54) = 0.85$, $p = .47$, indicating that the rate of learning about the geometric cues during the second stage of training was similar between males and females.

These data and accompanying statistics demonstrate a very similar pattern of learning to that of Experiment 2A. Whether the geometric cues are present but irrelevant, or entirely absent, appears to make little difference to the performances of males and females in this task. It seems likely that, regardless of gender, participants paid little attention to the irrelevant geometric cues whilst locating the hidden goal with respect to the landmark cues during Experiment 2A. Importantly, as with Experiment 2A, there was no difference between males and females in their ability to switch from a landmark-based to a geometry-based strategy. This leaves us to conclude that the difference in performance between males and females in Experiment 1 is not due to a more rapid strategy change by males. Having ruled out differences in strategy-switching ability as the cause of this gender difference, some evidence would need to be provided for the alternative explanation: that males learned more about the geometric cues during compound training than females. This geometry learning could then have led to an improved performance at locating the hidden goal with respect to the geometric cues, once the landmark cues had been made irrelevant. Experiment 3 was designed to test whether, after training with landmark and geometry cues in compound as in Experiment 1, males had learned more about the geometric cues than the females.

5.4 Experiment 3

Experiment 1 demonstrated that the transition from learning to locate a hidden goal with respect to both landmark and geometry cues, to learning to locate that goal based solely on geometry cues, affected females more than males. Experiments 2A and 2B demonstrated that, counter to an argument put forward by Sandstrom et al. (1998), this gender difference was not the result of males being able to switch between a landmark-based and geometry-based strategy more effectively. Experiment 3 aims to provide evidence of the alternative explanation: that the males in Experiment 1 learned more than females about the relevance of the geometric cues during compound training. In this experiment, participants were trained with a compound of landmark and geometry cues in the same manner as during Experiment 1. The landmark cues and the hidden goal were then removed for a single trial, and how much time participants spent searching for the hidden goal in the quadrant of the arena in which it was located during compound training was measured and compared against the time spent exploring in the opposite quadrant. Support for the theory that males learned more about the geometric cues during this compound training stage would be evidenced by males showing a stronger discrimination of correct and incorrect quadrants than females.

5.4.1 Method

5.4.1.1 Participants

Twenty participants completed this experiment, with equal numbers of males and females. The age range was 18-21, and there was no significant difference between the ages of males (*M* = 19, *SD* = 1) and females (*M* = 19, *SD* = 1), *t*(18) = .88, *p* = .39.

5.4.1.2 Apparatus

The apparatus used in this experiment was identical to that used in Experiments 1 and 2.

5.4.1.3 Procedure

Participants were trained for eight trials with a compound of landmark and geometry cues in the trapezium arena, in exactly the same manner as during the compound training stage of Experiment 1. Participants were then given a 45 s geometry test in the trapezium-shaped arena without any landmark cues present. The hidden goal was also absent during this trial, in order to determine where participants spent their time searching for this goal. Participants began this trial positioned in the centre of the shorter of the parallel walls, facing into the centre of the arena. Their search patterns were recorded and the time spent in the quadrant of the arena containing the goal location during training was compared with the time spent in the quadrant of the arena containing the mirror-opposite corner. See Figure 5.7 for a schematic of the design for Experiment 3.

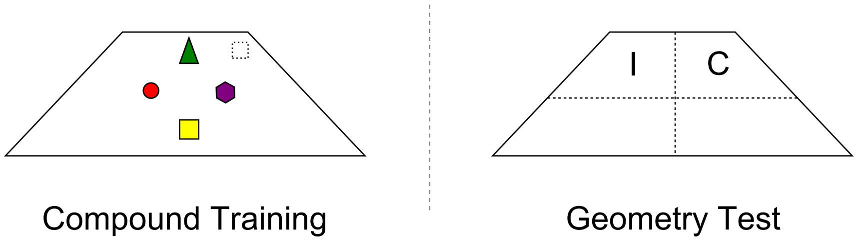


Figure 5.7: A not-to-scale schematic of the design of Experiment 3. The dashed square represents the location of the hidden goal during compound training. The ‘C’ represents the correct corner: the quadrant of the trapezium in which the hidden goal was located during training. The ‘I’ represents the incorrect corner: the mirror opposite of the correct corner, not containing the hidden goal during training.

5.4.2 Results and Discussion

5.4.2.1 Compound Training

The time taken to locate the hidden goal during compound training can be seen in Figure 5.8. There is an apparent decrease in latency to find the goal for both genders as training progressed, suggesting some learning about the location of the goal. Although there is a suggestion that males found the goal quicker than females overall, the high variance, especially for trial block 1, suggests that this difference may be small.

A mixed model ANOVA (Trial Block x Gender) of the average time taken by males and females to locate the hidden goal for each trial block confirmed these descriptions of the data. There was a significant main effect of trial block, $F(1, 18) = 53.5$, $p < .001$, with participants taking less time to find the hidden goal as

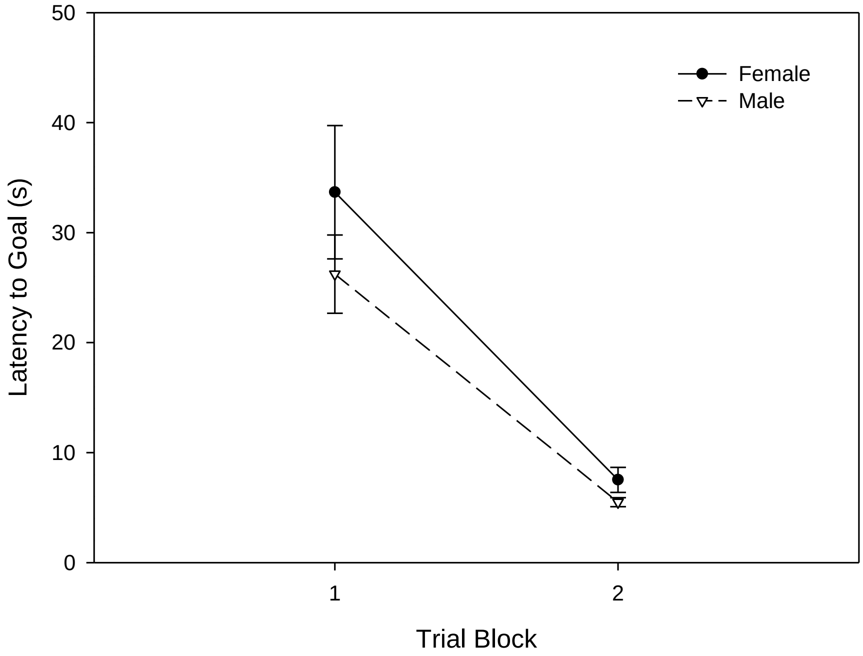


Figure 5.8: The time taken for participants to locate the hidden goal during compound training of Experiment 3, split by gender. Each data point represents the average of four successive trials, to equate for distance to the hidden goal from the starting location.

training progressed. There was neither a significant main effect of gender, *F*(1, 18) = 1.48, *p* = .24, nor an interaction between gender and trial block, *F*(1, 18) = 0.72, *p* = .41. This suggests that both males and females took a similar amount of time to find the hidden goal, regardless of the amount of training, and that the rate of learning about the location of the goal did not differ between the genders. Importantly, at the end of the eight trials of compound training, both males and females required the same amount of time to locate the hidden goal. A comparison should be made with the training data from Experiment 1, in which we saw the same equivalency between genders at the end of compound training. This lack of a difference is essential for it to be asserted that any differences evident in the test trial of this experiment are a result of inferior geometry learning, rather than a deficiency in motivation or ability to manipulate the apparatus.

5.4.2.2 Geometry Test

The time spent searching for the hidden goal in the correct and incorrect quadrants of the trapezium arena can be seen in Figure 5.9. Females spent a similar amount of time exploring each of the two quadrants. However, males spent more time searching for the goal in the quadrant of the arena that contained the goal during training, when compared with the mirror opposite quadrant, which had never contained the hidden goal.

A repeated measures ANOVA (Quadrant x Gender) of time spent in the correct and incorrect quadrants by males and females demonstrated a significant main effect of quadrant, *F*(1, 18) = 10.4, *p* = .005, with more time being spent searching for the hidden goal in the correct quadrant than the incorrect quadrant overall. Importantly, there was a significant interaction between quadrant and gender, *F*(1, 18) = 5.89, *p* = .03. An

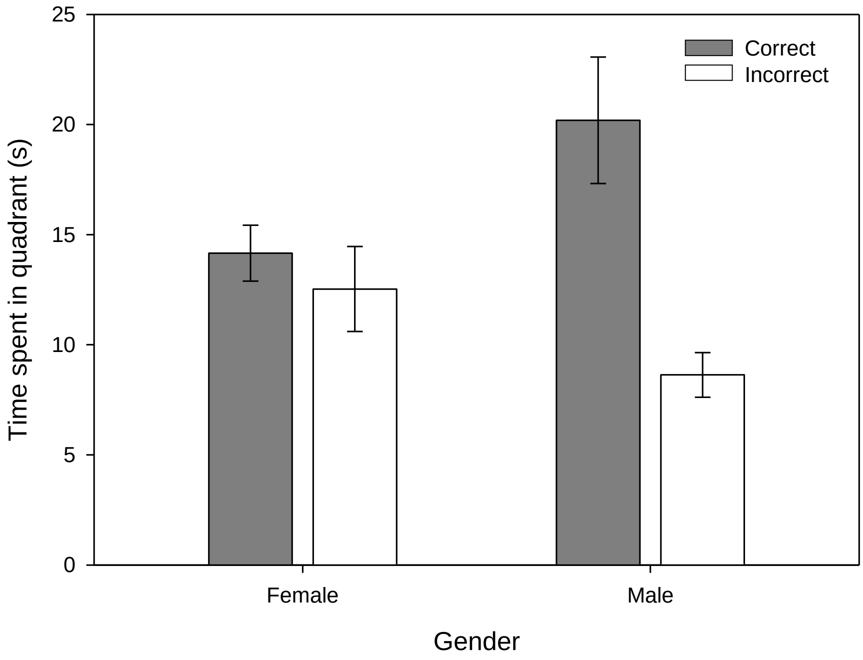


Figure 5.9: The time spent searching for the hidden goal in the quadrant of the trapezium that contained the goal during training (correct) and its mirror opposite quadrant, which did not contain the goal during training (incorrect).

analysis of the simple main effects for this interaction shows that males spent significantly more time searching for the hidden goal in the correct quadrant than the incorrect quadrant, $F(1, 18) = 16.0$, $p = .001$, whereas females did not display a preference for either quadrant, $F(1, 18) = 0.32$, $p = .58$. The difference in time spent exploring within the correct quadrant between genders approached significance, $F(1, 18) = 3.69$, $p = .07$, with a suggestion that males spent more time searching for the hidden goal in the correct quadrant than females. In addition, the difference in time spent searching within the incorrect quadrant between genders approached significance, $F(1, 18) = 3.20$, $p = .09$, suggesting that females spent longer searching for the goal in the incorrect quadrant than males. There was no significant main effect of gender, $F(1, 18) = 0.36$, $p = .55$.

These results demonstrate that when trained with both landmark and geometry cues, only males learned about the position of the hidden goal with respect to the geometric cues. This lack of learning about geometry by females occured despite the fact that they did learn to locate the hidden goal to the same extent as males when both landmark and geometry cues were present during training.

5.5 General Discussion

In Experiment 1 males and females were trained to locate a hidden goal with respect to a compound of landmark and geometry cues. Females were more affected than males when the landmark cues became irrelevant, taking significantly longer to locate the goal. There are two possible reasons for this gender difference: either males learned more about geometric cues during compound training than females, or males were able to switch the strategy they used to find the goal more quickly than females. Experiments 2A and 2B showed that when a direct strategy switch was required, from locating the hidden goal with respect to landmark cues to having to use geometry cues, there was no such gender difference, providing evidence against a gender difference based on strategy-switching. Experiment 3 gave support to the theory that the male superiority was a consequence of better geometry learning during the compound training stage. This geometry learning allowed males to locate the hidden goal more rapidly than females when only the geometric cues reliably indicated the goal’s location.

The results from this chapter refute the argument proposed by Sandstrom et al. (1998) that males are more adept at strategy-switching than females. However, Sandstrom et al.’s experiments contained the same confound as Experiment 1: the presence of geometric cues during the first stage of training that reliably indicated the goal’s location. Upon removing this confound it was observed that there was no difference in strategy-switching ability between the genders. That instead the difference was due to differential geometry learning between the genders is readily supported in the literature, in both animals (e.g., Rodriguez, Chamizo, & Mackintosh, 2011), and humans (e.g., Lövdén et al., 2007).

The data from this chapter go a long way in explaining the results of Chapter 4 Experiment 1, in which females failed to demonstrate the presence of within-compound associations between landmark and geometry cues. The same geometric cues were used in that experiment as in this chapter, and so it can be inferred that females learned little about the geometric cues present in that test of within-compound associations. Therefore, if little is learned about the geometric cues, it can hardly be expected that females would discriminate between them and thus demonstrate the presence of within-compound associations. Whether within-compound associations had formed between the geometric and landmark cues at all depends on the reason behind females showing little geometry learning. If the geometric cues had a very low salience for females, or if little attention had been paid to them, then it would not be expected that they would have been able to enter into within-compound associations. However, it has been demonstrated in a spatial task, at least in rats, that within-compound associations can form between a compound of cues in the absence of a reward, in a sensory pre-conditioning paradigm (Rhodes et al., 2009). Therefore, if the geometric cues were evident, but their relationship to the goal location was less realised by females, then it is still possible that they had entered into within-compound associations with the landmark cues. If this were the case, it would still be possible that these within-compound associations would be able to counteract the overshadowing effects that compound training with two cues should produce. For females trained with a compound of landmark and geometry cues, learning based on geometric cues could be boosted by evoked representations of the landmark cues, via the within-compound associations. No geometry-reward contingency is required for this boost, and therefore potentiation of geometry learning by concurrent training with landmark cues is conceivable, despite little being learned about the geometry itself. Therefore, the ability of females to discriminate between geometric cues for the group trained with a compound of landmark and geometry cues would be mostly a consequence of the formation of within-compound associations between those cues. It would not be trivial to demonstrate the presence of within-compound associations between landmark and geometry cues if the geometric cues were not readily associated with reward. However, one consequence of such associations could be asymmetrical counteraction of overshadowing. If landmark and geometry cues are trained in compound, and within-compound associations form between those cues, then experiencing a geometric cue alone should evoke a representation of the associated landmark cue. This representation should boost responding to the geometric cue, as a result of the landmark-reward association. This would counteract the overshadowing of geometric cues by the landmark cues that would be expected following compound training. However, experience of only the landmark cue following compound training should not produce the same effect, as the evoked representation of geometry should not affect the reward contingency. Therefore, counteraction of overshadowing of landmarks by geometry should not be expected. Whatever the merit of the above discussion, it should be noted that, from the results of this chapter, it cannot be asserted whether or not within-compound associations actually formed between landmark and geometry cues for females during Experiment 1 of Chapter 4. It is possible that they formed but were undetectable using the method employed, or that they did not form at all, presumably as a result of females learning little about the association between the geometric cues and the location of the hidden goal.

One finding apparent throughout all the experiments of this chapter is that males consistently located the hidden goal more quickly than females, regardless of the cues available with which to do this. This is a readily explicable result from Experiments 1 and 3, in which both landmarks and geometry cues were available for locating the goal. It has been demonstrated that males learn more about the geometric cues than females. Therefore, it follows that males could locate the goal based on both the landmark and geometry cues, whereas females would have had to rely solely on the landmark cues. However, for Experiments 2A and 2B, learning during the first stages must have been based only on landmark cues, as geometric cues were either not present or not reliable for locating the hidden goal. During these landmark-only training trials, males again demonstrated lower latencies to find the goal. Therefore, it is possible that in addition to showing superior geometry learning, males are also more proficient at navigating with respect to landmark cues than females. There is some evidence in the literature for this, at least in rat studies. Forcano, Santamaría, Mackintosh, and Chamizo (2009) found that when a single landmark indicated the location of a hidden goal, as long as that landmark was not directly over the goal location there was a male superiority in both time taken to find the goal during training trials, and time spent in the goal's previous location during extinction trials. In addition, Rodriguez, Aguilar, and Chamizo (2011) showed that when two landmark cues indicated the location of a hidden goal, but were positioned some distance away from each other and from the goal location, there were similar male advantages. The landmark cues in the experiments of this chapter were similar to those used by Forcano et al. and Rodriguez et al. in that the goal location was not coincident with the location of the landmarks, but rather it was required that distance and direction from the landmark cues had to be calculated to find the goal. It is possible, therefore, that males did show a superiority for learning locations with respect to landmark cues, in addition to their geometry superiority. Unfortunately, the experiments described in this chapter are unable to determine whether or not this was the case. However, a simple test would be to train both males and females with only landmark cues available to locate the hidden goal, as in Experiment 2B. A test trial could then be used to determine how long males and females spend searching for the now absent hidden goal in the location, with respect to the landmark cues, in which it was positioned during training.

However, the apparent gender difference may not be related to how much each gender had learned about the relationship between the available cues and the hidden goal. It is well documented that proficiency with experimental apparatus influences performance during human spatial learning tasks (e.g., Waller, 2000). Waller, Hunt, and Knapp (1998) demonstrated the influence of equipment proficiency by comparing the gender differences evident in a real-world task and its virtual equivalent. That the male superiority was greater in the virtual than the real-world task led the authors to conclude that a degree of the gender differences observed were a consequence of differences in equipment proficiency rather than in spatial ability. It has been reported that males are more experienced video gamers than females (Lucas & Sherry, 2004; Philips, Rolls, Rousse, & Griffiths, 1995) and that training females on action-based video games reduces the differences in spatial ability between the genders (Feng, Spence, & Pratt, 2007). This implies that the male superiority evident throughout this chapter was potentially, at least in part, due to a difference in the level of experience of virtual navigation situations.

It is not yet unequivocal whether males and females learn equally well about landmark cues within a virtual environment, and what proportion of apparent gender differences can be attributed to differences in equipment proficiency. However, neither of these lacunae detract from the main focus of this chapter. It has been demonstrated that males and females were able to switch the strategy they used to locate a hidden goal with equal merit and that the gender difference observed in Experiment 1 was in fact a consequence of males having learned more about the relevance of geometric cues during training. This superior geometry learning in males coherently explains the results of Chapter 4 Experiment 1, in which within-compound associations between geometric and landmark cues were evidenced only in male participants.

CHAPTER SIX

Discussion

In Chapter 2 it was shown that within-compound associations exist between landmark and geometry cues, and these within-compound associations are evident under the same circumstances in which both potentiation and a lack of overshadowing occur. It was argued that the extent to which the landmark overshadows the geometry during compound training determines whether or not the within-compound associations are able to counteract overshadowing strongly enough to produce potentiation.

In Chapter 3 the generality of the action of within-compound associations was established. It was asserted that if within-compound associations form between landmarks and geometry then reduced overshadowing of landmarks by geometry should also be observed. This was shown to be true, with geometric cues failing to either overshadow or potentiate learning about landmark cues. It was demonstrated that under the same circumstances in which this failure to observe cue competition occurred, landmark cues were able to evoke a representation of geometry cues with which they were paired in the manner required for within-compound associations to be the cause of the cue competition failure.

Chapter 4 established that within-compound associations also formed between landmark and geometry cues in human participants, albeit only in males. Females were shown to be able to form these associations in a non-spatial context, thus prompting further investigation into the nature of this spatial disparity between genders.

Chapter 5 demonstrated that the differences between males and females in spatial ability were a consequence of females being less able to learn about geometric information, rather than their ability to switch spatial strategy less flexibly than males. This can readily be explained associatively by appeal to a difference in the salience of geometric cues for males and females. The inability of females to form within-compound associations between landmark and geometry cues in Chapter 4 was therefore explainable under associative principles.

The remainder of this Discussion will address the main aims of this thesis presented in the Introduction. Firstly, it will be argued that spatial learning can best be described by appeal to the rules governing associative learning in other modalities. Secondly, that the rules by which spatial learning operates are not specific to such factors as species or gender.

6.1 Is spatial learning associative?

Contrary to the many previous failures to demonstrate cue competition in the spatial domain, this thesis has demonstrated that cue competition effects do occur between geometric and non-geometric cues. It is evident that geometry learning is potentiated by the concurrent presence of landmark cues. In addition, it is observed that geometric and non-geometric cues become associated together through compound training and changing the behaviour towards one of these cues in turn alters behaviour towards the other. All of the results observed within this thesis are explicable in terms of an associative, error-correction learning rule (e.g., Rescorla & Wagner, 1972), with the addition of the presence of within-compound associations forming between cues trained in compound (e.g., Van Hamme & Wasserman, 1994). This thesis adds to the growing body of evidence that learning with respect to landmark-based information is able to interact with learning about geometry-, or boundary-, based information. This stands counter to theories proposed by Cheng (1986), Gallistel (1990), and Doeller and Burgess (2008) who all invoke a special status for geometric, or boundary, information. Cheng and Gallistel assert that geometric and non-geometric information do not interact and, as such, learning about one proceeds without competition from the other. Doeller and Burgess suggest that learning about boundary information is not affected by concurrent non-geometric learning, an equally falsifiable position (Horne, Iordanova, & Pearce, 2010; Kosaki et al., 2013). It might be argued that although within-compound associations readily explain the presence of potentiation and lack of overshadowing in the experiments presented in this thesis, they have not been shown to be implicated causally in these effects. It must be accepted that a causal link between the presence of these associations and the presence of potentiation, or failure to observe overshadowing, would bolster the credibility of this argument. One example of how to achieve this causal link was proposed in the General Discussion of Chapter 2. However, there remain few alternative explanations for the data within this thesis on which proponents of non-associative spatial learning could cling. Timberlake et al.'s (2007) stable framework and Miller and Shettleworth’s (2007) feature enhancement accounts of potentiation are unable to explain the potentiation observed in Chapter 2. In addition, the geometric module hypothesis proposed by Cheng and Gallistel cannot explain either the potentiation of Chapter 2, or the fact that revaluing one of a trained compound of landmark and geometry cues causes the revaluation of the other in its absence. Therefore, even in the current absence of a causal link, within-compound associations, and by extrapolation associative learning, provide the most convincing account of the spatial learning effects present in this thesis.

The experiments presented in Chapter 5 provide an additional source of evidence for spatial learning being associative in nature. It was demonstrated that females, having been trained to locate a hidden goal with respect to a compound of landmark and geometry cues, were unable to locate the goal based solely on geometric information. This does not sit comfortably with suggestions of geometric information holding a special status above other cue modalities, especially those posited by Cheng (1986) and Gallistel (1990), which prescribe a primacy to learning about geometric information. If females learn with respect to a compound of landmark and geometry cues, but show no learning to the geometry, then this would suggest the opposite of a primacy for geometric information. Alternatively, if geometric cues hold no special status, as would be suggested by theories of associative learning, then a simple difference in the salience of these cues can readily explain the apparent gender difference. Should geometric cues be more salient for males than for females – as a consequence of any one of a variety of explanations, ranging from evolution to practice

– then associative theories would predict geometric cues to be learned about more completely by males than by females. Thus, again it can be seen that the results of spatial learning experiments can more readily be explained not by appeal to non-associative mechanisms, but by the application of established associative principles.

6.2 Are the Processes of Spatial Learning Ubiquitous?

There have been several demonstrations of landmarks failing to overshadow learning about geometry in humans (e.g., Redhead & Hamilton, 2007; Redhead et al., 2012), mirroring frequently observed effects in non-human animals. These results have previously constituted evidence for human spatial learning being non-associative in nature. However, in Chapter 4 it was shown that, as with non-human animals, there exists an associative mechanism by which these cue competition failures can be explained. The novel demonstration of within-compound associations between spatial and non-spatial cues in adult male humans would indicate that these previous failures to show overshadowing between similar cues can be explained associatively. This explanation would be analogous to that by which within-compound associations counteract the effects of overshadowing in non-human animals.

It could be argued that the landmarks in Experiment 1 of Chapter 4 do not act in the same way as the landmarks in the non-human demonstrations of within-compound associations. Rather than providing unique spatial cues that predict the location of the goal, information provided by the landmarks must be combined with geometric information to locate the goal. Although this does not undermine the premise that within-compound associations have been shown to form between spatial and non-spatial cues in human males, it is possible that these associations are not equivalent to those in the non-human studies. To address this concern, a modification could be made to Experiment 1 of Chapter 4. If, instead of occupying a position in the centre of the trapezium arena, the landmark cues were placed above the location of the goal, then both landmark and geometry cues would act as predictors of the goal's location. Revaluing one of these landmarks should then result in the revaluation of the geometry associated with that landmark. This would provide evidence of within-compound associations from a procedure more closely matched to that used in the non-human studies.

Although it was demonstrated in Chapter 4 that within-compound associations did not form between landmark and geometry cues in female participants, this does not detract from an argument that spatial learning is governed by associative principles in both humans and non-human animals. The demonstrations of within-compound associations in Chapters 2 and 3, and their role in both potentiation and failure of overshadowing, involved only male rats. No difference has therefore been demonstrated between the abilities of humans and rats to form within-compound associations between spatial and non-spatial cues. It was shown in Chapter 5 that the failure to observe these within-compound associations in female humans was a consequence of their inability to learn about geometric information. That female rats have poorer spatial abilities than male rats is well documented (e.g., Cimadevilla et al., 1999; Faraji et al., 2010; Rodriguez et al., 2010). Therefore, although their presence has not been tested, it would be of little surprise to find that within-compound associations between landmarks and geometry are not as evident in female rats as in male rats, owing to the female rats' reduced ability to learn about the relevance of the geometric cues.

The differences in spatial ability between males and females of either species present a possible method by which the effects of within-compound associations on counteracting overshadowing can be observed. Without the presence of within-compound associations to counteract the overshadowing that is typically predicted by associative theories, it might be expected that female humans, or rats, would show stronger overshadowing effects than males of those species, assuming that the geometric cues were salient enough to be learned about by females. Potential evidence of this is provided by Rodriguez, Chamizo, and Mackintosh (2011), who showed stronger overshadowing of geometry learning by female rats than by males. Unfortunately, however, due to the high variability in salience of geometric information between studies, weaker within-compound associations and stronger overshadowing for females would need to be demonstrated in studies using the same spatial and non-spatial cues. Further evidence would be provided for within-compound associations counteracting overshadowing if females were to show no within-compound associations and strong overshadowing, and males were to show within-compound associations and reduced overshadowing.

There is, however, an important factor to consider in the comparison between spatial learning studies between species. It has been argued throughout this thesis that the presence of within-compound associations counteracts the overshadowing that would typically be observed between cues trained in compound. It has also been asserted that it is the amount of initial overshadowing between the two cues that dictates whether potentiation or just a lack of overshadowing is observed. The greater the degree of overshadowing, the less likely the presence of the within-compound association is to counteract this strongly enough to produce potentiation. Indeed, with strong enough overshadowing, the presence of within-compound associations may not even be enough to counteract the overshadowing effect, and overshadowing may still be observed, albeit weaker than if within-compound associations were not present. In addition, although not observed in any experiments in this thesis, it is conceivable that the strength of within-compound associations is variable. One factor that may alter the degree to which overshadowing occurs, and also the strength of any within-compound associations that form between the cues, is that of motivation. In the watermaze tasks of Chapter 2 and 3, rats remained in a mildly aversive environment (swimming in the watermaze) until they found the goal location. However, in the virtual tasks of Chapters 4 and 5, humans were presented with no such aversive situation. It seems likely, therefore, that the rats would be more motivated to learn the relationships between the stimuli and the goal location and between the stimuli themselves. This would lead to the formation of stronger within-compound associations as a consequence of the aversive nature of the task, and may be the reason why potentiation is not an uncommon observation in studies involving rats in the watermaze, but why the same result is not seen in virtual experiments with human participants. Attempting to equate the motivational aspects of these tasks, for example by using an aversive auditory stimulus in virtual experiments with humans (Chamizo, Aznar-Casanova, & Artigas, 2003), may increase the likelihood of observing similar cue competition effects across a variety of species. This would further demonstrate the generality of associative principles to spatial learning, regardless of species.

6.3 Conclusion

The work presented within this thesis offers novel evidence that failure to observe typical cue competition effects between spatial and non-spatial information need not be reason to assume spatial learning to be non-associative. These results can be explained readily by the presence of within-compound associations and, by extension, associative learning. A similar mechanism has been shown to be present for the first time in humans, its presence providing an explanation for the failure to observe typical cue competition effects. The single failure to demonstrate the presence of these within-compound associations, in female humans, has been shown to be due to failure to learn about geometric information, an outcome supported by associative, but not non-associative theories.

All of the results within this thesis can more readily be explained by associative, rather than non-associative, principles. The work presented also demonstrates that a significant amount of other research, previously thought to constitute evidence for spatial learning being non-associative, can be explained in an associative manner. In addition, there appears to be little difference between the mechanisms underlying spatial learning between species. These are important steps in demonstrating that associative principles apply as equally to spatial learning as to learning in any other modality, and that the associative principles governing spatial learning are neither gender-, nor species-, specific.

REFERENCES

Abu-Ghazzeh, T. (1996). Movement and wayfinding in the King Saud University built environment: A look at freshman orientation and environmental information. *Journal of Environmental Psychology, 16,* 303-318.

Aitken, M. F. R., Larkin, M. J. W., Dickinson, A. (2001). Re-examination of the role of within-compound associations in the retrospective revaluation of causal judgements. *Quarterly Journal of Experimental Psychology, 54B,* 27-51.

Astur, R. S., Ortiz, M. L., & Sutherland, R. J. (1998). A characterization of performance by men and women in a virtual Morris water task: a large and reliable sex difference. *Behavioural Brain Research, 93,* 185-190.

Astur, R. S., Tropp, J., Sava, S., Constable, R. T., & Markus, E. J. (2004). Sex differences and correlations in a virtual Morris water task, a virtual radial arm maze, and mental rotation. *Behavioural Brain Research, 151,* 103-115.

Bell, S., & Saucier, D. (2004). Relationship among environmental pointing accuracy, mental rotation, sex, and hormones. *Environment and Behavior, 36,* 251-265.

Biegler, R., & Morris, R. G. M. (1999). Blocking in the spatial domain with arrays of discrete landmarks. *Journal of Experimental Psychology: Animal Behavior Processes, 25,* 341-351.

Cazzato, V., Basso, D., Cutini, S., & Bisiacchi, P. S. (2010). Gender differences in visuospatial planning: An eye movements study. *Behavioural Brain Research, 206,* 177-183.

Chamizo, V. D. (2003). Acquisition of knowledge about spatial location: assessing the generality of the mechanism of learning. *Quarterly Journal of Experimental Psychology, 56,* 102-113.

Chamizo, V. D., Aznar-Casanova, J. A., & Artigas, A. A. (2003). Human overshadowing in a virtual pool: Simple guidance is a good competitor against locale learning. *Learning and Motivation, 34,* 262-281.

Cheng, K. (1986). A purely geometric module in the rat's spatial representation. *Cognition, 23,* 149-178.

Cimadevilla, J. M., González-Pardo, H., López, L., Díaz, F., Cueto, E. G., García-Moreno, L. M., & Arias, J. L. (1999). Sex-related differences in spatial learning during the early postnatal development of the rat. *Behavioural Processes*, *46*, 159-171.

Clarke, J. C., Westbrook, R. F., & Irwin, J. (1979). Potentiation instead of overshadowing in the pigeon. *Behavioral and Neural Biology*, *25*, 18-29.

Cole, M. R., Gibson, L., Pollack, A., & Yates, L. (2011). Potentiation and overshadowing of shape by wall color in a kite-shaped maze using rats in a foraging task. *Learning and Motivation*, *42*, 99-112.

Dabbs, J. M., Chang, E. L., Strong, R. A., & Milun, R. (1998). Spatial ability, navigation strategy, and geographical knowledge among men and women. *Evolution and Human Behavior*, *19*, 89–98.

Dawson, J. L. M. (1972). Effects of sex hormones on cognitive style in rats and men. *Behavior Genetics*, *2*, 21-42.

Dickinson, A., & Burke, J. (1996). Within-compound associations mediate the retrospective revaluation of causality judgements. *Quarterly Journal of Experimental Psychology*, *49B*, 60-80.

Diez-Chamizo, V., Sterio, D., & Mackintosh, N. J. (1985). Blocking and overshadowing between intra-maze and extra-maze cues: A test of the independence of locale and guidance learning. *Quarterly Journal of Experimental Psychology*, *37B*, 235-253.

Doeller, C. F., & Burgess, N. (2008). Distinct error-correcting and incidental learning of location relative to landmarks and boundaries. *Proceedings of the National Academy of Sciences*, *105*, 5909-5914.

Doeller, C. F., King, J. A., & Burgess, N. (2008). Parallel striatal and hippocampal systems for landmarks and boundaries in spatial memory. *Proceedings of the National Academy of Sciences*, *105*, 5915-5920.

Durlach, P. L., & Rescorla, R. A. (1980). Potentiation rather than overshadowing in flavor-aversion learning: an analysis in terms of within-compound associations. *Journal of Experimental Psychology: Animal Behavior Processes*, *6*, 175-187.

Dwyer, D. M., Burgess, K. V., & Honey, R. C. (2012). Avoidance but not aversion following sensory preconditioning with flavors: a challenge to stimulus substitution. *Journal of Experimental Psychology: Animal Behavior Processes*, *38*, 359-368.

Einon, D. (1980). Spatial memory and response strategies in rats: Age, sex and rearing differences in performance. *Quarterly Journal of Experimental Psychology*, *32*, 473-489.

Faraji, J., Metz, G. A., & Sutherland, R. J. (2010). Characterization of spatial performance in male and female Long-Evans rats by means of the Morris water task and the ziggurat task. *Brain Research Bulletin*, *81*, 164-172.

Fellini, L., Schachner, M., & Morellini, F. (2006). Adult but not aged C57BL/6 male mice are capable of using geometry for orientation. *Learning and Memory*, *13*(4), 473-481.

Feng, J., Spence, I., & Pratt, J. (2007). Playing an action video game reduces gender differences in spatial cognition. *Psychological Science*, *18*, 850-855.

Forcano, L., Santamaría, J., Mackintosh, N. J., & Chamizo, V. D. (2009). Single landmark learning in rats: Sex differences in a navigation task. *Learning and Motivation*, *40*, 46-61.

Foreman, N., Stanton Fraser, D., Wilson, P. N., Duffy, H., & Parnell, R. (2005). Transfer of spatial knowledge to a two-level shopping mall in older people, following virtual exploration. *Environment and Behavior*, *37*, 275-292.

Galea, L. A. M., & Kimura, D. (1993). Sex differences in route learning. *Personality and Individual Differences*, *14*, 53-65.

Galef, B. G., & Osborne, B. (1978). Novel taste facilitation of the association of visual cues with toxicosis in rats. *Journal of Comparative and Physiological Psychology*, *92*, 907-916.

Gallistel, C. R. (1990). *The organization of learning*. Cambridge, MA: MIT Press.

Gaulin, S. J. C., & Fitzgerald, R. W. (1986). Sex differences in spatial ability: An evolutionary hypothesis and test. *American Naturalist*, *127*, 74-88.

Gaulin, S. J. C., & Fitzgerald, R. W. (1989). Sexual selection for spatial learning ability. *Animal Behavior*, *37*, 322-331.

Gouteux, S., Thinus-Blanc, C., & Vauclair, J. (2001). Rhesus monkeys use geometric and nongeometric information during a reorientation task. *Journal of Experimental Psychology: General*, *130*(3), 505-519.

Graham, M., Good, M. A., McGregor, A., & Pearce, J. M. (2006). Spatial learning based on the shape of environment is influenced by properties of the objects forming the shape. *Journal of Experimental Psychology: Animal Behavior Processes*, *32*, 44-59.

Gray, E. R., Bloomfield, L. L., Ferrey, A., Spetch, M. L., & Sturdy, C. B. (2005). Spatial encoding in mountain chickadees: features overshadow geometry. *Biology Letters*, *1*, 314-317.

Hamilton, D. A., Driscoll, I., & Sutherland, R. J. (2002). Human place learning in a virtual Morris water task: Some important constraints on the flexibility of place navigation. *Behavioural Brain Research, 129*, 159-170.

Hamilton, D. A., & Sutherland, R. J. (1999). Blocking in human place learning: Evidence from virtual navigation. *Psychobiology, 27*, 453-461.

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

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

Hegarty, M., Montello, D. R., Richardson, A. E., Ishikawa, T., & Lovelace, K. (2006). Spatial abilities at different scales: Individual differences in aptitude-test performance and spatial-layout learning. *Intelligence*, *34*, 151-176.

Hermer, L., & Spelke, E. (1996). Modularity and development: the case of spatial reorientation. *Cognition*, *61*(3), 195-232.

Horne, M. R., Iordanova, M. D., & Pearce, J. M. (2010). Spatial learning based on boundaries in rats is hippocampus-dependent and prone to overshadowing. *Behavioral Neuroscience*, *124*, 623-632.

Horne, M. R., & Pearce, J. M. (2009a). A landmark blocks searching for a hidden platform in an environment with a distinctive shape after extended pretraining. *Learning and Behavior, 37*, 167-178.

Horne, M. R., & Pearce, J. M. (2009b). Between-cue associations influence searching for a hidden goal in an environment with a distinctive shape. *Journal of Experimental Psychology: Animal Behavior Processes*, *35,* 99-107.

Horne, M. R., & Pearce, J. M. (2010). Conditioned inhibition and superconditioning in an environment with a distinctive shape. *Journal of Experimental Psychology: Animal Behavior Processes*, *36,* 381-394.

Horne, M. R., & Pearce, J. M. (2011). Potentiation and overshadowing of geometric cues provided by the shape of the environment. *Learning and Behavior, 39,* 371-382.

Jansen-Osmann, P., & Wiedenbauer, G. (2004). The representation of landmarks and routes in children and adults: A study in a virtual environment. *Journal of Environmental Psychology*, *24,* 347-357.

Kamin, L. J. (1969). Predictability, surprise attention, and conditioning. In B. A. Campbell & R. M. Church (Eds.), *Punishment and aversive behaviour* (pp. 279-296). New York: Appleton-Century-Crofts.

Kavaliers, M., Ossenkopp, K. P., Prato, F. S., Innes, D. G. L., Galea, L.A.M., & Kinsella, D. M. (1996). Spatial learning in deer mice: Sex differences and the effects of endogenous opioids and 60Hz magnetic fields. *Journal of Comparative Physiology*, *179*, 715-24.

Kavaliers, M., Ossenkopp, K. P., Galea, L. A. M., & Kolb, B. (1998). Sex differences in spatial learning and prefrontal and parietal cortical dendritic morphology in the meadow vole, *Microtus pennsylvanicus*. *Brain Research, 810,* 41-47.

Kelly, D. M., & Bischof, W. F. (2005). Reorienting in images of a three-dimensional environment. *Journal of Experimental Psychology: Human Perception and Performance*, *31*, 1391-1403.

Kelly, D. M., Spetch, M. L., & Heth, C. D. (1998). Pigeons' (Olumba Livia) encoding of geometric and featural properties of a spatial environment. *Journal of Comparative Psychology*, *112*, 259-269.

Kosaki, Y., Austen, J. M., & McGregor, A. (2013). Overshadowing of geometry learning by discrete landmarks in the water maze: Effects of relative salience and relative validity of competing cues. *Journal of Experimental Psychology: Animal Behavior Processes*, *39*(2), 126-139.

Kozlowski, L. T., & Bryant, K. J. (1977). Sense of direction, spatial orientation, and cognitive maps. *Journal of Experimental Psychology: Human Perception and Performance*, *3,* 590-598.

Lacreuse, A., Herndon, J. G., Killiany, R. J., Rosene, D. L., & Moss, M. B. (1999). Spatial cognition in rhesus monkeys: Male superiority declines with age. *Hormones and Behavior, 36,* 70-76.

Leonard, B., & McNaughton, B. L. (1990). Spatial representation in the rat: conceptual, behavioral, and neurophysiological perspectives. In R. P. Kesner & D. S. Olton (Eds.), *Neurobiology of Comparative Cognition* (pp. 363-422). Hillsdale NJ: Lawrence Erlbaum.

Levy, L. A., Astur, R. S., & Frick, K. M. (2005). Men and women differ in object memory but not performance of a virtual radial maze. *Behavioral Neuroscience, 199,* 853-862.

Linn, M. C., & Peterson, A. C. (1985). Emergence and characterization of sex differences in spatial ability: A meta-analysis. *Child Development*, *56*, 1479-1498.

Lourenco, S. F., Addy, D., Huttenlocher, J., & Fabian, L. (2011). Early sex differences in weighting geometric cues. *Developmental Science*, *14,* 1365-1378.

Lövdén, M., Herlitz, A., Schellenbach, M., Grossman-Hutter, B., Krüger, A., & Lindenberger, U. (2007). Quantitative and qualitative sex differences in spatial navigation. *Scandinavian Journal of Psychology, 48,* 353-358.

Lubow, R. E., & Moore, A. U. (1959). Latent inhibition: The effect of non-reinforced preexposure to the conditional stimulus. *Journal of Comparative and Physiological Psychology*, *52*, 415-419.

Lucas, K., & Sherry, J. L. (2004). Sex differences in video game play: A communication-based explanation. *Communication Research*, *31*, 499-523.

Mackintosh, N. J. (1976). Overshadowing and stimulus intensity. *Animal Learning and Behavior, 4*, 186-192.

McGregor, A., Horne, M. R., Esber, G. O., & Pearce, J. M. (2009). Absence of overshadowing between a landmark and geometric cues in a distinctively shaped environment: A test of Miller and Shettleworth (2007). *Journal of Experimental Psychology: Animal Behavior Processes*, *35*, 357-371.

Melchers, K. G., Lachnit, H., & Shanks, D. R. (2004). Within-compound associations in retrospective revaluation and in direct learning: A challenge for comparator theory. *Quarterly Journal of Experimental Psychology*, *57B,* 25-53.

Miller, N. Y., & Shettleworth, S. J. (2007). Learning about environmental geometry: An associative model. *Journal of Experimental Psychology: Animal Behavior Processes*, *33*, 191-212.

Mishima, N., Higashitani, F., Teraoka, K., & Yoshioka, R. (1986). Sex differences in appetitive learning of mice. *Physiology and Behavior*, *37*, 263-268.

Moffat, S. D., Hampson, E., & Hatzipantelis, M. (1998). Navigation in a “virtual” maze: Sex differences and correlation with psychometric measures of spatial ability in humans – relation to psychometrically-defined spatial functions. *Evolution and Human Behavior, 19,* 73-87.

Mueller, S. C., Jackson, C. P., & Skelton, R. W. (2008). Sex differences in a virtual water maze: An eye tracking and pupillometry study. *Behavioural Brain Research*, *193*, 209-215.

Newhouse, P., Newhouse, C., & Astur, R. (2007). Sex differences in visual-spatial learning using a virtual water maze in pre-pubertal children. *Behavioural Brain Research*, *183*, 1-7.

O’Keefe, J., & Nadel, L. (1978). *The hippocampus as a cognitive map.* Oxford, UK: Clarendon Press.

Overman, W. H., Pate, B. J., Moore, K., Peuster, A. (1996). Ontogeny of place learning in children as measured in the radial arm maze, Morris search task, and open field task. *Behavioral Neuroscience*, *110*, 1205-1228.

Passini, R., Rainville, C., Marchand, N., & Joanette, Y. (1995). Wayfinding in dementia of the Alzheimer's type: Planning abilities. *Journal of Clinical and Experimental Psychology*, *17*, 820-832.

Pavlov, I. P. (1927). *Conditioned reflexes*. Oxford: Oxford University Press.

Pearce, J. M. (1994). Similarity and discrimination: a selective review and a connectionist model. *Psychological Review, 101*, 587-607.

Pearce, J. M., Ward-Robinson, J., Good, M., Fussell, C., & Aydin, A. (2001). Influence of a beacon on spatial learning based on the shape of the test environment. *Journal of Experimental Psychology: Animal Behavior Processes*, *27*, 329-344.

Pearce, J. M., Graham, M., Good, M. A., Jones, P. M., & McGregor, A. (2006). Potentiation, overshadowing, and blocking of spatial learning based on the shape of the environment. *Journal of Experimental Psychology: Animal Behavior Processes*, *32*, 201-214.

Phillips, C. A., Rolls, S., Rouse, A., & Griffiths, M. D. (1995). Home video game playing in schoolchildren: A study of incidence and patterns of play. *Journal of Adolescence*, *18*, 687-691.

Prados, J., Alvarez, B., & Reynolds, G. (2011). Spatial integration in human geometry learning. *Behavioural Brain Research*, *224*, 297-304.

Rankin, C. H. (2000). Context conditioning in habituation in the nematode *Caenorhabditis elegans*. *Behavioral Neuroscience*, *114*, 496-505.

Ratliff, K. R., & Newcombe, N. S. (2005). Human spatial reorientation using dual task paradigms. *Proceedings of the Annual Cognitive Science Society, 27*, 1809-1814.

Redhead, E. S., & Hamilton, D. A. (2007). Interaction between locale and taxon strategies in human spatial learning. *Learning and Motivation, 38*, 262-283.

Redhead, E. S., & Hamilton, D. A. (2009). Evidence of blocking with geometric cues in a virtual watermaze. *Learning and Motivation*, *40*, 15-34.

Redhead, E. S., Hamilton, D. A., Parker, M. O., Chan, W., & Allison, C. (2012). Overshadowing of geometric cues by a beacon in a spatial navigation task. *Learning and Behavior*.

Redhead, E. S., Roberts, A., Good, M., & Pearce, J. M. (1997). Interaction between piloting and beacon homing by rats in a swimming pool. *Journal of Experimental Psychology: Animal Behavior Processes*, *23*, 340-350.

Rescorla, R. A., & Freberg, L. (1978). The extinction of within-compound flavor associations. *Learning and Motivation, 9*, 411-427.

Rescorla, R. A., & Wagner, A. R. (1972). A theory of pavlovian conditioning: variations in the effectiveness of reinforcement and nonreinforcement. In A.H. Black, & W.F. Prokasy (Eds.), *Classical Conditioning II* (pp. 64–99). Appleton-Century-Crofts.

Rhodes, S. E. V., Creighton, G., Killcross, A. S., Good, M., & Honey, R. C. (2009). Integration of geometric with luminance Information in the rat: evidence from within-compound associations. *Journal of Experiment Psychology: Animal Behavior Processes, 35*, 92-98.

Richardson, A. E., Montello, D. R., & Hegarty, M. (1999). Spatial knowledge acquisition from maps and from navigation in real and virtual environments. *Memory and Cognition*, *27*, 741–750.

Roberts, A. D. L., & Pearce, J. M. (1998). Control of spatial behavior by an unstable landmark. *Journal of Experimental Psychology: Animal Behavior Processes, 24*, 172-184.

Roberts, A. D. L., & Pearce, J. M. (1999). Blocking in the Morris swimming pool. *Journal of Experimental Psychology: Animal Behavior Processes*, *25,* 225-235.

Rodrigo, T., Chamizo, V. D., McLaren, I. P. L., & Mackintosh, N. J. (1997). Blocking in the spatial domain. *Journal of Experimental Psychology: Animal Behavior Processes*, *23,* 110-118.

Rodriguez, C. A., Aguilar, R., & Chamizo, V. D. (2011). Landmark learning in a navigation task is not affected by the females rats' estrus cycle. *Psicológica, 32*, 279-299.

Rodriguez, C. A., Chamizo, V. D., & Mackintosh, N. J. (2011). Overshadowing and blocking between landmark learning and shape learning: The importance of sex differences. *Learning and Behavior*, *39,* 324-335.

Rodriguez, C. A., Torres, A., Mackintosh, N. J., & Chamizo, V. D. (2010). Sex differences in the strategies used by rats to solve a navigation task. *Journal of Experimental Psychology: Animal Behavior Processes*, *36*, 395-401.

Rose, F. D., Attree, E. A., Brooks, B. M., Parslow, D. M., Penn, P. R., & Ambihaipahan, N. (2000). Training in virtual environments: transfer to real world tasks and equivalence to real task training. *Ergonomics*, *43,* 494-511.

Rosenthal, H. E. S., Norman, L., Smith, S. P., & McGregor, A. (2012). Gender-based navigation stereotype improves men's search for a hidden goal. *Sex Roles*, *67,* 682-695.

Ruddle, R. A., Payne, S. J., & Jones, D. M. (1997). Navigating buildings in “desk-top” virtual environments: Experimental investigations using extended navigational experience. *Journal of Experimental Psychology: Applied*, *3*, 143-159.

Rusiniak, K. W., Hankins, W. G., Garcia, J., & Brett, L. P. (1979). Flavor-illness aversions: potentiation of odor by taste in rats. *Behavioral and Neural Biology*, *25*, 1-17.

Sandstrom, N. J., Kaufman, J., & Huettel, S. A. (1998). Males and females use different distal cues in a virtual environment navigation task. *Cognitive Brain Research*, *6*, 351-360.

Seymoure, P., Dou, H., & Juraska, J. M. (1996). Sex differences in radial maze performance: Influence of rearing environment and room cues. *Psychobiology*, *24*, 33-37.

Shepard, R. N., & Metzler, J. (1971). Mental rotation of three-dimensional objects. *Science*, *171*, 701-703.

Silverman, I., & Eals, M. (1992). Sex differences in spatial abilities: Evolutionary theory and data. In J. H. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 531–549). New York: Oxford Press.

Sovrano, V. A., Bisazza, A., & Vallortigara, G. (2002). Modularity and spatial reorientation in a simple mind: encoding of geometric and nongeometric properties of a spatial environment by fish. *Cognition*, *85*, B51-B59.

Timberlake, W., Sinning, S. A., & Leffel, J. K. (2007). Beacon training in a water maze can facilitate and compete with subsequent room cue learning in rats. *Journal of Experimental Psychology: Animal Behavior Processes*, *33*, 225-243.

Tolman, E. C. (1948). Cognitive maps in rats and men. *Psychological Review*, *55*, 189-208.

Vadillo, M. A., Castro, L., Matute, H., & Wasserman, E. A. (2008). Backward blocking: The role of within-compound associations and interference between cues trained apart. *Quarterly Journal of Experimental Psychology*, *61*, 185–193.

Vallortigara, G., Zanforlin, M., & Pasti, G. (1990). Geometric modules in animals’ spatial representations: A test with chicks (*Gallus gallus domesticus*). *Journal of Comparative Psychology*, *104*, 248-254.

Van Hamme, L. J., & Wasserman, E. A. (1994). Cue competition in causality judgments: The role of nonpresentation of compound stimulus elements. *Learning and Motivation*, *25*, 127-151.

Voyer, D., Voyer, S., & Bryden, M. P. (1995). Magnitude of sex differences in spatial abilities: A meta-analysis and consideration of critical variables. *Psychological Bulletin*, *117,* 250-270.

Wall, P. L., Botly, L. C. P., Black, C. K., & Shettleworth, S. J. (2004). The geometric module in the rat: independence of shape and feature learning in a food finding task. *Learning and Behavior*, *32*, 289-298.

Waller, D. (2000). Individual differences in spatial learning from computer-simulated environments. *Journal of Experimental Psychology: Applied*, *6*, 307-321.

Waller, D., Hunt, E., & Knapp, D. (1998). The transfer of spatial knowledge in virtual environment training. *Presence: Teleoperators and Virtual Environments*, *7*, 129-143.

Wang, R. F., & Spelke, E. S. (2002). Human spatial representation: insights from animals. *Trends in Cognitive Sciences*, *6*(9), 376-382.

Wang, R. F., & Spelke, E. S. (2003). Comparative approaches to human navigation. In K. Jeffrey (Ed.), *The Neurobiology of Spatial Behavior* (pp. 119-143). Oxford University Press.

Wasserman, E. A., & Berglan, L. R. (1998). Backward blocking and recovery from overshadowing in human causal judgement: The role of within-compound associations. *Quarterly Journal of Experimental Psychology*, *51B*, 121-138.

Wilson, P. N., & Alexander, T. (2010). Enclosure shape influences cue competition effects and goal location learning. *Quarterly Journal of Experimental Psychology*, *63*, 1552-1567.