Buckley, Matthew G. (2015) Mechanisms of shape-based spatial learning. PhD thesis, University of Nottingham.

Access from the University of Nottingham repository:
http://eprints.nottingham.ac.uk/30702/7/Matt%20Buckley%20Thesis.pdf

Copyright and reuse:

The Nottingham ePrints service makes this work by researchers of the University of Nottingham available open access under the following conditions.

- Copyright and all moral rights to the version of the paper presented here belong to the individual author(s) and/or other copyright owners.
- To the extent reasonable and practicable the material made available in Nottingham ePrints has been checked for eligibility before being made available.
- Copies of full items can be used for personal research or study, educational, or not-for-profit purposes without prior permission or charge provided that the authors, title and full bibliographic details are credited, a hyperlink and/or URL is given for the original metadata page and the content is not changed in any way.
- Quotations or similar reproductions must be sufficiently acknowledged.

Please see our full end user licence at:
http://eprints.nottingham.ac.uk/end_user_agreement.pdf

A note on versions:

The version presented here may differ from the published version or from the version of record. If you wish to cite this item you are advised to consult the publisher’s version. Please see the repository url above for details on accessing the published version and note that access may require a subscription.

For more information, please contact eprints@nottingham.ac.uk

Mechanisms of Shape-based Spatial Learning

Matthew G. Buckley

Thesis submitted to University of Nottingham for the degree of Doctor of Philosophy.

December, 2015

Abstract

The ability to navigate to important locations is fundamental to both human and non-human animals. The experiments presented in this thesis were designed to address three key predictions generated from the model of navigation proposed by Miller and Shettleworth (2007, 2008, 2013): First, cue competition effects should be observed between local geometric information and landmarks; Second, the attention paid to geometric and non-geometric cues within an environment should not be modifiable; Third, organisms should not learn about a global representation of the shape of the environment. The results of the blocking experiments reported in Chapter 2 demonstrate that local geometric cues compete with non-geometric cues for control over navigational behaviour, in a manner consistent with the Miller-Shettleworth model. The intradimensional-extradimensional shift and learned predictiveness effects reported in Chapters 3 and 4, respectively, are not consistent with the notion that the attention paid to geometric and non-geometric cues is fixed. The experiments reported in Chapter 5 provide core evidence that humans encode a global representation of the shape of the environments in which they navigate, a result that is also not consistent with the Miller-Shettleworth model. These results suggest that, at best, the model proposed by Miller and Shettleworth (2007, 2008, 2013) provides an incomplete explanation for spatial learning behaviour. In order to account for the data reported in Chapters 3 and 4, it is necessary for the Miller-Shettleworth model to permit changes in the attention paid to navigational stimuli. Additionally, in order to

account for the data presented in Chapter 5, it appears necessary to assume that humans encode a global Euclidean representation of the shape of the environments in which they navigate. The challenge for future work will be to determine the precise manner in which multiple representations of environmental geometry support effective navigation.

Summary

Navigation is a core component of everyday life for us all. Knowing where we are, where we have been, and where we want to go is fundamental to negotiating the world around us. According to the geometric module hypothesis (Cheng, 1986; Gallistel, 1990), organisms encode a global representation of the shape in which they navigate, and this representation is not prone to interference from other cues. In order to be consistent with this prediction, a landmark must never overshadow, or block, learning about the boundary shape of an environment. A number of cue competition experiments have demonstrated that landmarks do not interfere with learning about geometric information. There are, however, instances in which landmarks have overshadowed, or blocked, learning about the boundary shape of an environment. In order to provide a reconciliation of these contradictory findings, Miller and Shettleworth (2007, 2008, 2013) proposed an associative model of spatial learning based on the Rescorla-Wagner (1972) learning algorithm, in which geometric and non-geometric cues are encoded as representational elements. By permitting geometric and non-geometric information to compete with each other for control over behaviour, the Miller-Shettleworth model can successfully explain instances in which a non-geometric cue interferes with learning about the boundary shape of an environment. Importantly, through a process termed feature enhancement, the model also successfully explains instances in which non-geometric information fails to overshadow, or block, learning about the boundary shape

of an environment. Despite providing a compellingly simple reconciliation of the contradictory findings observed in spatial cue competition experiments, few experiments have been conducted to test the assumptions made by the Miller-Shettleworth model. Consequently, the experiments presented in this thesis were designed to address three key predictions generated from the model proposed by Miller-Shettleworth.

First, as noted above, the model assumes that geometric information is permitted to compete with non-geometric information for associative strength. It might, therefore, be expected that cue competition effects should be observed between local geometric information and landmarks, and the experiments reported in Chapter 2 tested this prediction. Experiment 1 replicated previous findings (Lew et al., 2014) that humans transfer navigational behaviour from a rectangle-shaped environment to a kite-shaped environment (and vice versa), a result that provides evidence for the encoding of local geometric information during spatial navigation. In Experiments 2 and 3, it was observed that learning about a non-geometric cue blocked, and was blocked by, learning about local geometric information. This reciprocal blocking is consistent with the associative model of spatial navigation proposed by Miller and Shettleworth (2007, 2008, 2013).

Second, as a consequence of using the Rescorla-Wagner model as its starting point, the model proposed by Miller and Shettleworth (2007, 2008, 2013) inherits the assumption that the associability of a navigational stimulus (or a stimulus dimension) is fixed. Consequently, the model predicts that the salience of geometric and non-geometric cues within an environment is not modifiable (cf. Mackintosh, 1975). In Chapter 3, this claim was explored with three intradimensional-extradimensional (ID-ED) shift experiments, designed to examine whether it was possible to modify the salience of spatial cues. In Experiments 4 and 5, participants were first required to find a hidden goal using information provided by the shape of the arena, or landmarks integrated into the arena boundary (Experiment 4), or within the arena itself (Experiment 5). Participants were then transferred to a different-shaped arena that contained novel landmarks, and were again required to find a hidden goal. In both experiments, participants who were navigating on the basis of cues that were from the same dimension that was previously relevant (intradimensional shift) learned to find the goal significantly faster than participants who were navigating on the basis of cues that were from a dimension that was previously irrelevant (extradimensional shift). In order to explain the observed ID-ED effect, it is necessary to permit changes in attention to relevant and irrelevant stimuli (e.g. Esber & Haselgrove, 2011; Le Pelley, 2004; Mackintosh, 1975) and, thus, these experiments were not consistent with the Miller-Shettleworth model. Experiment 6 replicated Experiment 5, and also assessed participants' recognition of the global-shape of the navigated arenas. Participants in all groups successfully recognised the shape of the environments in which they had previously navigated, although recognition was attenuated when landmarks had been relevant to navigation during the experiment. This result provides further evidence that it is necessary to permit changes in the attention paid to stimuli within an environment. More interestingly, however, that participants could recognise the shape of the environments in which they had previously navigated suggests they may have encoded a global representation of the shape of the environments and, furthermore, that this representation is modifiable by stimulus relevance.

As noted previously, overshadowing designs have commonly been used to test whether learning about landmark information interferes with learning about shape information provided by the boundary walls of an environment. Whilst a number of studies have shown that landmarks are not able to overshadow learning about shape information, some have shown that landmarks can, in fact, overshadow learning about shape information. Given that the experiments in Chapter 3 demonstrated that it was possible to alter the attention paid to spatial stimuli, the experiments reported in Chapter 4 were designed to assess if the relative salience of shape and landmark information could account for the discrepant results of overshadowing studies. In Experiment 7, participants were first trained that either the landmarks within an arena (landmark-relevance), or the shape information provided by the boundary walls of an arena (shape-relevance), were relevant to finding a hidden goal. In a subsequent stage, when novel landmark and shape information were both made relevant to finding the hidden goal, landmarks dominated behaviour for those given landmark-relevance training, whereas shape information dominated behaviour for those given shape-relevance training. Experiment 8, which was conducted without relevance training, revealed that the landmark cues unconditionally dominated behaviour in the stage 2 arena used in Experiment 7. It is possible to account for the results of these two experiments, and the conflicting results from previous overshadowing experiments, with associative models that incorporate an attention variant (cf. Miller and Shettleworth, 2007, 2008, 2013)

Third, although the Miller-Shettleworth model does not explicitly state what is learned about the boundary shape of an environment, it permits learning to elements that are present at individual corners. Consequently, the model does not advance the possibility that organisms learn about a global representation of the shape of the environment in which they navigate. The experiments reported in Chapter 5 were designed to test whether humans can navigate on the basis of global-shape information. Participants were trained to navigate to a hidden goal on one side of an arena (e.g. the inside) before being required to find the same point on the alternative side (e.g. the outside). Participants navigated to the appropriate goal location, both when inside and outside the arena, but only when the shape of the arena remained the same between training and test (Experiments 9a and 9b). When the arena shape was transformed between these stages, participants were lost (Experiments 10a and 10b). When training and testing was conducted on the outside of two different-shaped arenas that shared local geometric cues, participants once again explored the appropriate goal location (Experiment 11). These results provide core evidence that humans encode a global representation of the shape of the environments in, or around, which they navigate.

Taken together, the results presented in this thesis suggest that, at best, the model proposed by Miller and Shettleworth (2007, 2008, 2013) provides an incomplete explanation for spatial learning behaviour. The results of the blocking experiments reported in Chapter 2 provide evidence that local geometric cues compete with non-geometric cues for control over spatial navigational behaviour, in a manner consistent with the Miller-Shettleworth model. The ID-ED and learned predictiveness effects observed in Chapters 3 and 4, respectively, are not consistent with the notion that the salience of geometric and non-geometric cues within an environment is fixed. Consequently, in order to account for these results, it is necessary for the Miller-Shettleworth model to permit changes in the attention paid to stimuli in manner envisaged by attentional models of learning (e.g. Esber & Haselgrove, 2011; Le Pelley, 2004; Mackintosh, 1975). Finally, in order to account for the data presented in Chapter 5, it appears necessary to assume that humans encode a global Euclidean representation of the shape of the environments in, or around, which they navigate. The challenge for future work will be to determine the precise manner in which these multiple representations of environmental geometry support effective navigation, and how these representations interact with non-geometric information, such as landmarks.

Publications

The data contained in this thesis have been published, or submitted for publication, as follows:

Chapter 2

Buckley, M. G., Smith, A. D., & Haselgrove, M. (Accepted). Blocking spatial navigation across environments that have a different shape. *Journal of Experimental Psychology: Animal learning and Cognition.*

Chapter 3

Buckley, M. G., Smith, A. D., & Haselgrove, M. (2014). Shape shifting: Local landmarks interfere with navigation by, and recognition of, global shape. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 40,* 492-510.

Chapter 4

Buckley, M. G., Smith, A. D., & Haselgrove, M. (2015). Learned predictiveness training modulates biases towards using boundary or landmark cues during navigation. *Quarterly Journal of Experimental Psychology*, *68*(6), 1183-1202.

Chapter 5

Buckley, M. G., Smith, A. D., & Haselgrove, M. (Submitted). Thinking outside of the box: Human spatial-navigation requires multiple representations of the shape of the environment. *Cognitive Psychology*

Acknowledgements

First and foremost, thanks to my supervisors Mark Haselgrove and Alastair Smith. I could not have wished for a better supervision team, and to mention all the ways you have helped me over the past four years would double the length of this thesis. Please know that I am truly grateful for all your support. Without your guidance, I would not be the scientist that I am today. Thanks also to the members of the Behavioural Neuroscience group. All of the data in thesis was presented at our lab meetings, and the discussions we had were most helpful. In addition, I am grateful to Jasper Robinson for the comments and suggestions you have made as my internal examiner.

The research in this thesis was funded by a studentship from the Economic and Social Research Council, without which I would not have had the opportunity to conduct the experiments reported here. During my time in Nottingham, I have worked with a number of excellent students. Thanks to Harriet Scales and Jane Taylor for their help with running Experiment 9, and also to Luke Holden and Stuart Spicer for their help with conducting some of the future work that is mentioned in the general discussion of this thesis.

Finally, I am grateful for the social life that my friends and family have provided outside of my work. I am, in particular, extremely thankful for the loving support of Natalia Stanulewicz, and her endless patience during my final months of writing.

Table of Contents

List of Figures 12

List of Tables 14

Chapter 1: General Introduction 15

1.1 Navigation and associative learning 17
1.2 Cognitive maps 20
1.3 Evidence that shape is special 29
1.4 Evidence that shape is not special 35
1.5 Global and local encoding of shape information 46
1.6 The Miller-Shettleworth model 52
1.7 Structure of the thesis 58

Chapter 2: Blocking of spatial navigation 60

2.1 Experiment 1 65
2.2 Experiment 2 80
2.3 Experiment 3 92
2.4 General discussion 106

Chapter 3: Landmarks interfere with navigation by global-shape 112

3.1 Experiment 4 119
3.2 Experiment 5 132
3.3 Experiments 6a and 6b 141
3.4 General discussion 155

Chapter 4: Boundary and landmark biases during navigation 162

4.1 Experiment 7 170
4.2 Experiment 8 183
4.3 General discussion 193

Chapter 5: Multiple representations of environmental shape 201

5.1 Experiments 9a and 9b 206
5.2 Experiments 10a and 10b 223
5.3 Experiment 11 236
5.4 General discussion 243

Chapter 6: General Discussion 251

6.1 Future work 260
6.2 Conclusion 273

References 275

List of Figures

Chapter 1: General Introduction

Figure 1.1 Environments used by Tolman et al. (1946) 21
Figure 1.2 Haywood et al. (2004) blocking experiment 33
Figure 1.3 Pearce et al. (2006) blocking experiment 39
Figure 1.4 McGregor et al. (2006) shape-transformation experiment 50

Chapter 2: Blocking of spatial navigation

Figure 2.1 Schematic views of Experiment 1 arenas 70
Figure 2.2 Environments used in Experiment 1 71
Figure 2.3 Mean acquisition latencies of Experiment 1 73
Figure 2.4 Mean time spent in zones at test of Experiment 1 75
Figure 2.5 Design of Experiment 2 82
Figure 2.6 Environments used in Experiment 2 85
Figure 2.7 Mean stage 1 and stage 2 latencies of Experiment 2 88
Figure 2.8 Mean time spent in zones at test of Experiment 2 90
Figure 2.9 Environments used in Experiment 3 96
Figure 2.10 Design of Experiment 3 98
Figure 2.11 Mean stage 1 and stage 2 latencies of Experiment 3 100
Figure 2.12 Mean time spent in zones at test of Experiment 3 102

Chapter 3: Landmarks interfere with navigation by global-shape

Figure 3.1 Environments used in Experiment 4 122
Figure 3.2 Design of Experiments 4, 5, and 6 126
Figure 3.3 Mean stage 1 latencies of Experiment 4 128
Figure 3.4 Mean stage 2 latencies of Experiment 4 129
Figure 3.5 Environments used in Experiments 5 and 6 135
Figure 3.6 Mean stage 1 latencies of Experiment 5 136
Figure 3.7 Mean stage 2 latencies of Experiment 5 138
Figure 3.8 Stimuli for shape recognition task of Experiment 6 146
Figure 3.9 Mean stage 1 latencies of Experiment 6 148
Figure 3.10 Mean stage 2 latencies of Experiment 6 149
Figure 3.11 Mean percent correct shape recognition of Experiment 6 152

Chapter 4: Boundary and landmark biases during navigation

Figure 4.1 Design of Experiment 7 176
Figure 4.2 Mean stage 1 latencies of Experiment 7 178
Figure 4.3 Mean stage 2 latencies of Experiment 7 179
Figure 4.4 Mean time spent in zones at test of Experiment 7 181
Figure 4.5 Mean stage 1 and stage 2 latencies of Experiment 8 189
Figure 4.6 Mean time spent in zones at test of Experiment 8 191

Chapter 5: Multiple representations of environmental shape

Figure 5.1	Design of Experiment 9a	208
Figure 5.2	Design of Experiment 9b	209
Figure 5.3	Environments used in Experiments 9, 10, and 11	211
Figure 5.4	Schematic views of Experiment 9, 10, and 11 arenas	215
Figure 5.5	Mean acquisition latencies, and mean time spent in zones at test, of Experiment 9a	219
Figure 5.6	Mean acquisition latencies, and mean time spent in zones at test, of Experiment 9b	221
Figure 5.7	Design of Experiment 10a	227
Figure 5.8	Design of Experiment 10b	228
Figure 5.9	Mean acquisition latencies, and mean time spent in zones at test, of Experiment 10a	230
Figure 5.10	Mean acquisition latencies, and mean time spent in zones at test, of Experiment 10b	232
Figure 5.11	Design of Experiment 11	238
Figure 5.12	Mean acquisition latencies, and mean time spent in zones at test, of Experiment 11	241

Chapter 6: General Discussion

Figure 6.1	Design used to assess overshadowing of global-shape representations	263
Figure 6.2	Design used to assess if local-shape representations are particularly prone to generalisation decrement	265

List of Tables

Chapter 1: General Introduction

Table 1.1 Evidence that landmarks do not overshadow boundaries 42
Table 1.2 Evidence that landmarks do overshadow boundaries 43
Table 1.3 Evidence that landmarks do not block boundaries 44
Table 1.4 Evidence that landmarks do block boundaries 45

Chapter 2: Blocking of spatial navigation

Table 2.1 First-choice data for group rectangle-kite of Experiment 1 76
Table 2.2 First-choice data for group kite-rectangle of Experiment 1 76

Chapter 6: General Discussion

Table 6.1 Instructions that promote the formation of a cognitive map 270

Chapter 1

General Introduction

The ability to learn the location of important places in the world is a fundamental ability for both non-human and human animals alike. Consider, for instance, a rat foraging for food before needing to make a return journey to its nest. The necessity of being able to accurately locate the burrow is clear. Without knowledge of the burrow's exact location, much of the energy the rat gained from consuming the food would be wasted by searching for the burrow. Learning the location of specific places within an environment is important for humans, also. Negotiating the daily commute between home and work requires precise knowledge of the location of these two places. Accordingly, the mechanisms by which organisms navigate to significant places within an environment have been widely studied. Experiments have shown that a plethora of stimuli can be used to aid navigating to a particular place, which include the slope of the floor (Nardi & Bingman, 2009; Nardi, Newcombe, & Shipley, 2011; Nardi, Nitsch, & Bingman, 2010), internally derived cues such as vestibular information (e.g. Wallace, Hines, Pellis, & Whishaw, 2002), movement kinematics (Loomis et al., 1993), somesthetic information (Lavenex & Lavenex, 2010), as well as visual cues afforded by an environment, such as the shape of boundary walls (e.g. Doeller & Burgess, 2008; Pearce, Ward-Robinson, Good, Fussell, & Aydin, 2001), and landmarks that are both distal and proximal to a goal location (Prados, Redhead, & Pearce, 1999; Roberts & Pearce, 1998; Save & Poucet, 2000). Landmarks are typically conceived of as discrete objects within an environment, such as a distinctive tree or building, whereas, boundary cues, such as a cliff face or the shape created by a walled enclosure, are distinct from landmarks as they tend to confine movement within a particular space (Lew, 2011; Pearce, 2009).

1.1 Navigation and associative learning

As well as identifying the cues which may aid navigating to a particular location within an environment, it is also important to understand how animals learn about those cues in the first place. Following Lloyd Morgan's Canon (1894), which states that the behaviour of animals should not be interpreted in terms of higher psychological processes if it can be interpreted with simpler psychological processes, associative learning provides a natural starting point for this endeavour. Associative learning theories are considered to provide a general, all-purpose, mechanism by which multiple species of animals may learn about any stimuli within their environment. Prototypically, stimuli within an environment are permitted to compete with each other for an associative link with important events that occur within the environment. Two hallmark phenomena stemming from this assumption of cue competition are overshadowing and blocking, which have been found using a variety of different species and stimuli (Bitterman, 2000). Overshadowing occurs when two, or more, stimuli are simultaneously paired with an outcome, which restricts learning about each stimulus (Pavlov, 1927). For instance, presenting two cues (X and Y) in a compound usually restricts what is learned about cues X and Y, relative to learning about cue X or Y paired with the outcome in isolation. In this instance, the presence of cue Y in the compound stimulus is said to have overshadowed learning about cue X in compound, and vice versa. Blocking occurs when one cue of a compound stimulus has been previously paired with an outcome, which prevents learning about the other cue that is simultaneously presented in the compound (Kamin, 1969). For instance, if training in which a compound (AB) signals an outcome is preceded by training in which only cue A signals the outcome, little will be learned about cue B, relative to learning about cue B paired with the outcome in an overshadowing control condition. Here, cue A is said to have blocked learning about cue B.

Associative learning theories, in their simplest form (e.g. Rescorla & Wagner, 1972), can explain a number of findings that have been observed in the spatial domain. For instance, a number of experiments have found that landmark cues compete with each other for an association with a navigational goal. For instance, in an experiment conducted by Redhead, Roberts, Good, and Pearce (1997), rats were placed into a circular pool of water, and were trained to locate a submerged platform. For rats given overshadowing training, the location of the platform was signalled by landmark cues that were beyond the boundary walls of the pool, and a beacon attached to the platform. For rats given control training, however, the location of the platform was signalled only by the distal landmark cues. In a test trial in which the platform and the beacon attached to it were removed, rats given overshadowing training spent significantly less time searching in the quadrant of the pool that had contained the platform, relative to rats given control training. Consequently, the presence of the beacon had restricted what rats in the overshadowing group had learned about the distal landmark cues.

In a blocking experiment conducted by Rodrigo, Chamizo, McLaren, and Mackintosh (1997), rats were required to learn the location of a submerged platform with respect to landmarks that were placed beyond the boundary walls of a circular pool. In stage 1 of the experiment, rats in the blocking group were trained to locate the platform with three landmarks (ABC), before an additional landmark (X) was added to the environment for stage 2 training. Rats in the control group received only stage 2 training, such that they learned the location of the platform with all four landmarks (ABCX) present. Test trials conducted with landmarks ABC revealed that rats in both the blocking and control groups spent an equivalent amount of time searching in the quadrant of the pool that had previously contained the platform. Importantly, however, test trials conducted with landmarks ACX revealed that the blocking group spent less time searching in the quadrant of the pool that had contained the platform, relative to the control group, an effect consistent with the notion that initial training with landmarks ABC had prevented learning about landmark X in the blocking group.

The clear implication of the experiments described above is that, consistent with the predictions of associative learning theories, landmark cues are able to both overshadow (see also: Chamizo, Aznar-Casanova, & Artigas, 2003; Chamizo, Manteiga, Rodrigo, & Mackintosh, 2006; Gould-Beierle & Kamil, 1999; Leising, Garlick, & Blaisdell, 2011; Sanchez-Moreno, Rodrigo, Chamizo, & Mackintosh, 1999) and block (see also: Biegler & Morris, 1999; Cheng & Spetch, 2001; Leising, Wong, Ruprecht, & Blaisdell, 2014; Roberts & Pearce, 1999; Rodrigo, Arall, & Chamizo, 2005; Stahlman & Blaisdell, 2009) learning about other landmark cues. As will be seen in this chapter, it is generally accepted that learning about landmark cues within an environment is consistent with the rules of associative learning (e.g. Doeller & Burgess, 2008), however, there is no such consensus with regards to how learning about the boundary shape of an environment proceeds. A number of theories of navigation have, historically, suggested that animals form cognitive maps, a representation of an environment in which learning is not governed by the principles of associative learning. As will be seen in the coming section, a number of theories clearly predict that learning about the boundary shape of an environment is immune to overshadowing and blocking effects.

1.2 Cognitive maps

The notion that animals may encode a non-associative cognitive map of their environment can be traced back to the work of Tolman. In an experiment conducted by Tolman, Ritchie, and Kalish (1946), rats were trained to run down one arm of a maze, across a circular table top, and then around a series of bends in a second arm of the maze, in order to reach a food reward (see Figure 1.1, top panel). Following this training, the meandering second arm of the maze was blocked, and a number of straight arms were added in its place (see Figure 1.1, bottom panel). The majority of the rats, when faced with this new environment, ran down the arm that led directly to the rewarded location. When discussing these results, Tolman (1948) argued that rats would have been unable to choose the novel arm of the maze that led directly to the rewarded location if, during training, they had learned only a single route to the rewarded location by associating a series of stimuli (e.g. views) with responses (e.g. turn left). Instead, it was suggested that the training trials allowed rats to learn that the food reward was at a specific location within the room. Importantly, in order to choose the novel arm of the maze that led directly to the rewarded location, Tolman suggested that the rats must have acquired a map-like representation of the environment.

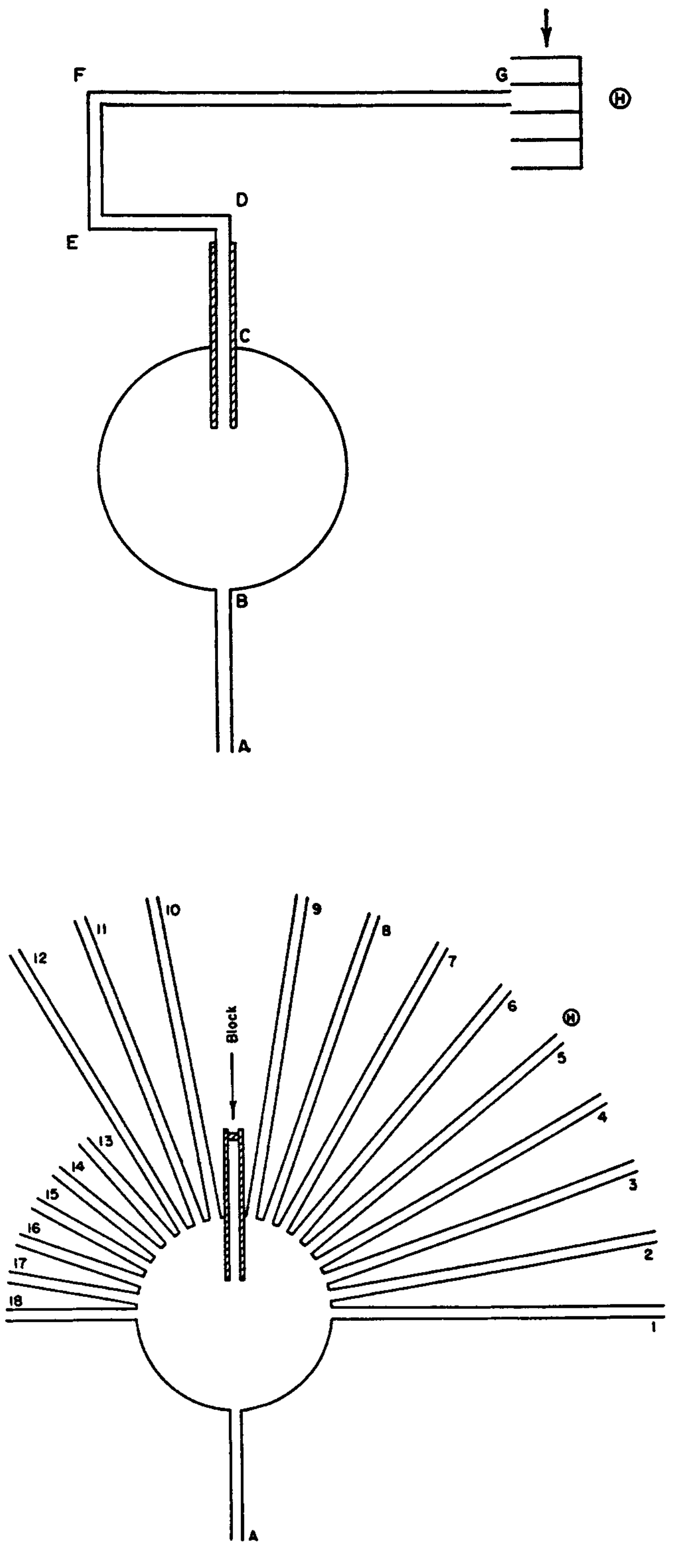


Figure 1.1. Training (top) and testing (bottom) apparatus used by Tolman, et al. (1946).

Tolman, however, did not clearly specify the conditions under which a cognitive map was acquired, or what information was contained within the map. It is, therefore, difficult to experimentally test the cognitive map as he proposed it. This lack of specificity was rectified by a theory proposed by O'Keefe and Nadel (1978), in which a hippocampal-based locale system was argued to be responsible for generating an allocentric cognitive map of the environment in which an animal navigates. This cognitive map holds information about the objects within an environment, and important places within the environment. Being allocentric in nature, the cognitive map is centred on the external environment. Consequently, the map is said to be view-point independent, as locations are defined in relation to objects in the environment, not the position of the navigator (see Burgess, 2006, 2008; Wang & Spelke, 2002). A non-hippocampal taxon system operates egocentrically, and is responsible for encoding a number of stimulus-response associations that may be sequentially ordered to form a route through an environment. Being egocentric in nature, this taxon system is centred on the navigator and, consequently, it is view-point dependent, such that locations are defined relative to the body axes of the navigator at a given position (see Burgess, 2006, 2008; Wang & Spelke, 2002). Learning in the taxon system occurs associatively, such that the response to a stimulus that signals a positive or negative outcome is to approach or avoid that stimulus, respectively. Learning in the locale system, however, is not governed by associative principles. Instead, cognitive maps are built, and later updated, by exploration of the environment. As an animal navigates through an environment, misplace detectors signal if a previously encountered object is now missing from the environment or, conversely, if a novel object has been added to the environment. Importantly, such changes to the environment are rapidly represented within the cognitive map, without any interference from other cues that are present.

The model proposed by O'Keefe and Nadel (1978) makes two key predictions that appear inconsistent with recent experimental data. First, the model expects that any discrepancies between the location of a landmark in an environment, and the expected location of that landmark within the cognitive map of that environment, to result in rapid updating of the location of the landmark within cognitive map. This makes the locale system particularly sensitive to variability within an environment, and it follows that it should not be possible to learn about a landmark that changes location, as there would always be a discrepancy between the actual location of the landmark within the environment, and the expected location of the landmark within the cognitive map. Results that are not consistent with this prediction were reported by McGregor, Horne, Esber and Pearce (2009). In Experiment 3, one group of rats learned to navigate to a submerged platform that was always located under a black spherical landmark, the location of which changed on a trial-by-trial basis such that it did not remain in a stable location relative to the square pool, or the distal cues surrounding the pool. In order to successfully navigate to the platform, therefore, rats must have relied on the moving landmark, as only it maintained a stable relationship with the goal on each trial (see also: Cuell, Good, Dopson, Pearce, & Horne, 2012; Hayward, Good, & Pearce, 2004; Hayward, McGregor, Good, & Pearce, 2003; Horne, Iordanova, & Pearce, 2010; Horne & Pearce, 2011; Pearce et al., 2001; Pearce, Graham, Good, Jones, & McGregor, 2006; Prados et al., 1999; Redhead, Prados, & Pearce, 2001). It may, however, be possible to reconcile the behaviour observed by McGregor et al. (2009) with the theory proposed by O'Keefe and Nadel (1978) if it was assumed that, in circumstances where animals are required to learn about a stimulus that does not maintain a constant position within the environment, behaviour is controlled by the taxon system. Consequently, the behaviour of rats in the experiment conducted by McGregor et al. (2009) would not have been controlled by a cognitive map, but instead rats would have learned to approach the moving black landmark as it signalled a positive outcome.

Second, as learning in the locale system depends only on exploration of an environment, any updates to the cognitive map of that environment should be immune to competition effects from other cues. That is, once a novel landmark is encountered, it should be added to the cognitive map without any interference from the cues that are already contained within the map. Consequently it should not be possible to observe overshadowing, or blocking, of learning within the cognitive map. As seen earlier, however, landmarks have been observed to overshadow (e.g. Redhead et al., 1997), and block (e.g. Rodrigo et al., 1997), learning about other landmarks. For instance, in an experiment by Roberts and Pearce (1999), rats in a blocking group were trained to find a submerged platform that had a landmark attached to it, within a circular pool of opacified water that was surrounded by a curtain. Once the rats had learned to swim to the platform in this first stage, the curtains that surrounded the pool were opened, such that the rats could now see the distal cues that were present in the experimental room. In this second stage of the experiment, the rats again had to swim to the submerged platform, the location of which was now signalled by both the landmark attached to it and the distal cues within the room. According to the theory proposed by O'Keefe and Nadel (1978), these distal cues should be added to a cognitive map that already represents the circular pool and the submerged platform. To see if rats in the blocking group had learned the location of platform with respect to the distal cues, they were given test trials in which the platform and landmark were not present. Compared to a control group that received only stage 2 training (Experiment 1), rats in the blocking group spent significantly less time in the quadrant of the pool that had previously contained the platform during the test trial. In contrast to the proposals of O'Keefe and Nadel (1978), therefore, learning the location of the platform with respect to the landmark attached to it blocked learning about the subsequently introduced distal cues.

Instances of cue competition between landmarks are difficult to reconcile with the proposals of O'Keefe and Nadel (1978), as interference effects between landmarks that signal a goal location are not expected. More recent cognitive mapping theories, however, might explain demonstrations of cue competition between landmarks. Gallistel (1990) suggested that a cognitive map represents the geometric relations among surfaces within the environment (p. 103), and it was argued that this was advantageous because, whilst the appearance of landmarks such as trees may change through the seasons (hence varying in their validity as a stimulus), the geometric relations among objects within an environment will remain constant. The notion that a cognitive map of an environment represents only geometric information within the environment raises the possibility that it is only learning about geometric information, and not landmarks, that is immune to cue competition effects.

According to Gallistel (1990), learning about the geometric properties of an environment occurs within a *geometric module*. This proposal followed the work of Cheng (1986), who conducted a series of experiments in which landmarks did not interfere with learning about the boundary shape of an environment. Cheng trained rats to find food that was hidden in one corner of a rectangle-shaped arena that contained a distinctive landmark in each corner. In order to find the food, rats could rely on the geometric information provided by the rectangle-shaped arena, or on the unique landmarks located in each corner. Relying on the geometric information provided by the rectangle-shaped arena would lead rats to search in either the correct corner, or in the diametrically opposite corner that was geometrically identical to the correct corner. The four unique landmarks, however, disambiguated all the corners of the rectangle from each other. Relying on the unique landmarks, then, would lead rats to search only in the correct corner. Following training, the landmarks were removed from the arena, and rats continued to search in both the correct and diametrically opposite corners more often than in the remaining two corners. Consequently, the presence of the more predictive landmark cues did not seem to preclude learning that was based upon the less predictive geometry of the rectangle (Cheng, 1986, see also: Margules & Gallistel, 1988). It must be noted, however, that it is somewhat difficult to interpret the results of this experiment without comparing the behaviour of rats to a control group that learned only about the geometric properties of the environment. Nevertheless, on the basis of these results, Cheng suggested that animals acquire a global representation of the geometry of the environment in which they navigate. This geometric information, moreover, is processed in a dedicated module that is impervious to the influence of other cues, such as landmarks. This position was championed by Gallistel (1990), who, in the context of discussing Cheng's data, suggested:

> "...this organ [the geometric module] constitutes a module in Fodor's (1983) sense; it works only with certain kinds of information, even under circumstances where other kinds of readily perceptible data are highly relevant to successful performance. Fodor termed this property of the module impenetrability." (Gallistel, 1990, p. 208.).

It should be noted that neither Cheng (1986), nor Gallistel (1990), clearly outlined the rules that govern learning about landmark cues within an environment. According to Doeller and Burgess (2008), however, learning about landmark cues proceeds in a manner consistent with associative learning theories. In contrast, and consistent with the proposals of the geometric module, learning to the boundary of an environment occurs in a non-associative manner. The boundary walls of an environment were afforded a special status by Doeller and Burgess on the basis of the results they observed in overshadowing and blocking experiments conducted in a virtual environment. In these experiments, learning about the boundaries of the environment overshadowed, and blocked, learning about a landmark within the environment. In contrast, learning about the landmark failed to overshadow, or block, learning about the environmental boundaries. The environmental boundaries, therefore, appeared immune to both hallmark associative cue competition effects (see also: Bullens et al., 2010). In addition, when participants completed the navigation task in a brain imagining study, it was found that hippocampal regions were active when participants were navigating on the basis of the environmental boundary, whereas, dorsal striatal areas were active when participants were navigating on the basis of the intramaze landmark (Doeller, King, & Burgess, 2008). On the basis of these findings, it was suggested that learning about environmental boundaries and landmark information occurs in separate systems. Learning about landmarks is said to occur in a striatal system, and is governed by standard associative learning principles. Learning about the boundaries of an environment, however, occurs in a hippocampal system, and is said to occur incidentally (Doeller & Burgess, 2008). Like the geometric module, then, learning about the boundary walls of an environment, which necessarily provide the shape of the environment, should occur even in the presence of equivalently, or more predictive landmarks.

In summary, the theories reviewed in this section afford shape cues provided by the boundary walls of an environment a special status during learning, and this has led to two contentious issues, each of which will each be addressed in the coming sections. First, both the geometric module hypothesis (Cheng, 1986; Gallistel, 1990, Wang & Spelke, 2002, 2003) and the proposals forwarded by Doeller and Burgess (2008: see also Doeller, et al., 2008), predict that the presence of landmarks in an environment should not interfere with learning about the boundary shape of an environment. The second issue, perhaps more fundamentally, surrounds the exact nature in which the boundary shape of an environment is encoded. According to the geometric module, when navigating through an environment, animals encode a global, allocentric, representation of the shape in which they navigate (Cheng, 1986; Gallistel, 1990). As will be seen later, however, it is possible to explain navigational behaviour without assuming animals encode this global representation of shape.

1.3 Evidence that shape is special

In associative learning theories, overshadowing and blocking effects are thought to represent the fact the one cue can reduce what is learned about a second cue (e.g. Esber & Haselgrove 2011; Le Pelley, 2004; Mackintosh, 1975; Pearce & Hall, 1980; Rescorla & Wagner, 1972). Consequently, cue competition designs have been ideally suited to assessing whether the presence of, say, landmarks can interfere with learning about the boundary shape of an environment.

Taking overshadowing experiments first, a number of experiments conducted with non-human animals have shown that the presence of landmark cues does not restrict learning about the boundary shape of an environment. For instance, Hayward et al. (2003) trained rats in an overshadowing group to find a submerged platform that was located in one corner of a rectangle-shaped pool and, also, underneath a distinctive landmark. Rats in a control group were given training that ensured that the geometric cues that signalled the platform location gained maximum control over behaviour. To achieve this, a submerged platform was located in each of the geometrically correct corners of the rectangle-shaped arena, but with no landmark present during training. A test trial, in which the platform was removed from the arena, revealed that both groups preferentially searched in the corners of the environment that had signalled the goal location, over corners that had not signalled the goal location. Importantly, though, overshadowing and control rats spent an equivalent amount of time searching in these correct corners of the environment. Clearly, then, the presence of the landmark during training did not restrict learning about the geometric cues that signalled the location of the platform in the overshadowing group, a result that has been replicated, using a variety of different boundary shapes and landmarks, in rats (Graham, Good, McGregor, & Pearce, 2006; Hayward et al., 2004; McGregor et al., 2009; Pearce et al., 2001) and pigeons (e.g. Kelly, Spetch, & Heth, 1998).

Overshadowing experiments conducted with adult humans have also demonstrated that landmark information does not restrict learning about the boundary shape of an environment. Redhead and Hamilton (2007) trained participants to navigate to a goal in an isosceles triangle-shaped virtual environment which contained two landmarks that were located in the corners at either end of the shortest wall. For participants in an overshadowing group, the two landmarks were unique and, thus, the goal could be found on the basis of both the boundary shape of the pool and the landmarks within the pool. For a control group, the two landmarks within the pool were identical, thus, only the boundary shape of the pool signalled the goal location. Following training, a test trial in which both the goal and the landmarks were removed from the arena was administered, and participants were allowed to search for 45 seconds. During this test trial, participants in both groups preferentially searched in the corner that had contained the goal, compared to the corner at the other end of the shortest wall of the triangular arena, which did not previously contain the goal. Crucially, both groups traversed equivalent distances in the corner of the arena where the goal was located during training. Consistent with the observations of Haywood et al. (2003), then, the presence of a predictive landmark did not restrict learning about the boundary shape of an environment in human participants (see also: Bullens et al., 2010; Doeller & Burgess, 2008; Doeller et al., 2008).

A number of reorientation studies, conducted with children, offer further support to the notion that the boundary shape of an environment is processed in a dedicated module that does not operate according to associative learning principles. For example, in experiments conducted by Hermer and Spelke (1994, 1996), children were required to find a hidden object located in one of the four corners of a rectangle-shaped arena that was 1.22 x 1.91 metres, and that comprised three white walls and one blue wall. Associative learning theories, in this scenario, would expect children to learn the exact location of the hidden toy with respect to the unique wall that unambiguously signals its location. Children, however, failed to use this landmark information and, instead, searched equally often in the geometrically equivalent corners of the experimental environment (see also: Hermer-Vazquez, Moffet, & Munkholm, 2001; Wang, Hermer, & Spelke, 1999). Similar observations have also been observed in a wide variety of animals, including fish (e.g. Sovrano, Bisazza, & Vallortigara, 2003; Vargas, López, Salas, & Thinus-Blanc, 2004), mice (e.g. Fellini, Schachner, & Morellini, 2006), and chicks (e.g. Vallortigara, Zanforlin, & Pasti, 1990). It must be noted, however, that it is difficult to interpret the results of these studies as there was not an appropriate control group in which participants were required to learn only about the shape of the environment. Without such a control group, the possibility that the landmark cue had only partially overshadowed learning about the shape of the environment cannot be ruled out.

Consistent with the findings from overshadowing designs, blocking experiments conducted with non-human animals have also demonstrated that landmarks do not interfere with learning about the boundary shape of an environment. In an experiment conducted by Hayward et al. (2004), rats were, initially, required to locate one of two submerged platforms in a rectangle-shaped environment that contained two landmarks. In both the blocking and control groups, the landmarks were always located near to a submerged platform. Between trials, however, these landmarks were moved within the rectangle-shaped arena (see Figure 1.2). Consequently, for both groups, only the landmarks signalled a goal location during stage 1 training. In a second stage of the experiment, rats in both groups were required to navigate to a submerged platform that was located in a geometrically unique corner at the base of a triangle-shaped pool. For rats in the blocking group only, the landmark that signalled the location of platform in stage 1 was presented in stage 2 and, again, it signalled the location of the platform (see Figure 1.2). The presence of this landmark was expected to prevent rats in the blocking group from learning the location of the platform with respect to the triangle-

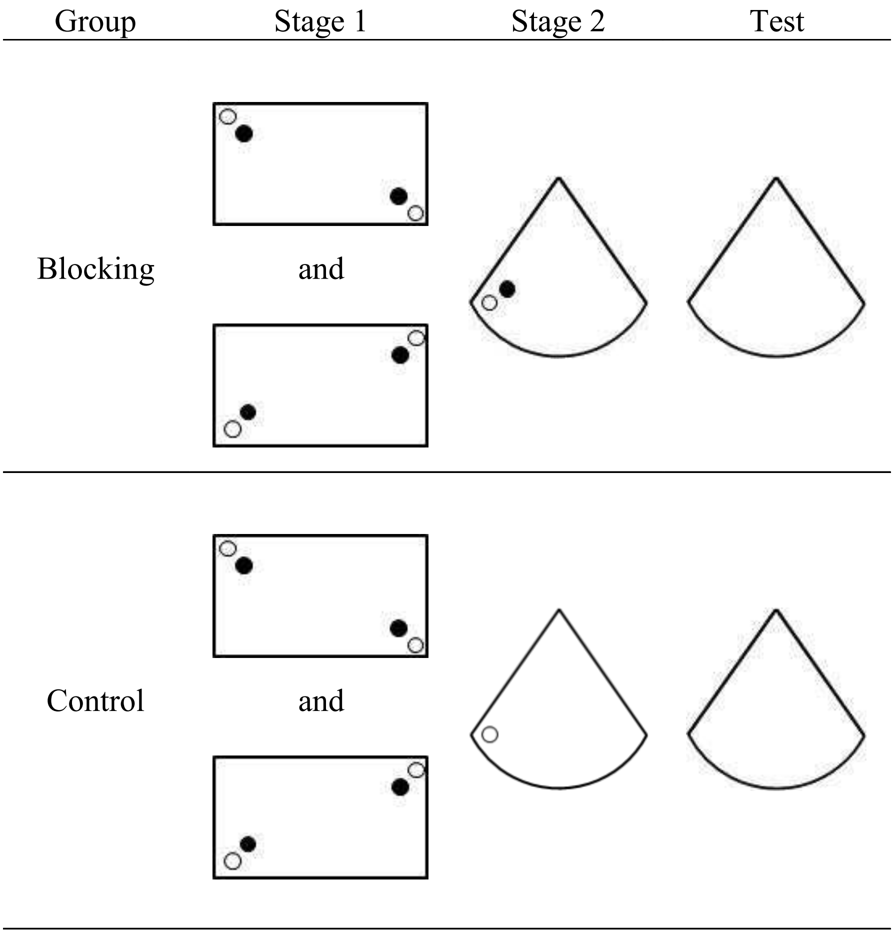


Figure 1.2. Design of the blocking experiment conducted by Haywood et al. (2004). White circles represent a submerged platform, and black circles represent a landmark cue.

shaped boundary. Contrary to this prediction, in a test trial conducted in the absence of the platform and landmark, rats in the blocking group preferentially searched in the quadrant of the pool that had previously contained the platform, relative to an adjacent quadrant at the base of the triangular-shaped arena. Notably, the blocking and control groups spent an equivalent amount of time searching in the quadrant of the pool that had previously contained the platform. Consequently, initial training in which a landmark was established as a predictor of a goal location failed to block learning about subsequently introduced geometric information that also signalled the goal location, a finding that has been replicated in a other studies conducted with rats (see also: Hayward et al., 2003; Pearce et al., 2001; Wall, Botly, Black, & Shettleworth, 2004).

Landmarks have been shown to not block learning about the boundary shape of an environment in experiments conducted with humans, also. In a virtual reality experiment conducted by Redhead and Hamilton (2009), participants in a blocking group were trained, in stage 1 of the experiment, to locate a goal that was signalled by one of two distinctively-coloured landmarks that were contained within circular environment. Following this training, participants were placed into an isosceles triangle-shaped arena. The same two landmarks that were presented in stage 1 were also present in this arena, one at either end of the shortest boundary wall. In this stage of the experiment, the goal that participants were required to locate was signalled by the same landmark as in stage 1 and, also, by the unique geometry of the corner in which it was now located. A control group received trials identical to that given to the blocking group in stage 2, however, unlike the blocking group, control participants were given no training in stage 1. A test trial conducted in an isosceles triangle-shaped arena, that contained no landmarks or goals, revealed that both groups preferentially searched in the zone of the arena that previously contained the goal, relative to a zone located at the other end of the shortest wall of the environment. Importantly, both the blocking and control groups spent an equivalent amount of time in the zone of the arena where the goal was previously located. In accord with observations with rats, therefore, learning the location of a goal with respect to a landmark cue failed to prevent human participants subsequently learning the location of the goal with respect to boundary shape information (see also: Doeller & Burgess, 2008).

In summary, the studies reviewed above show that landmarks do not seem to interfere with learning about the boundary shape of environments. A lack of cue competition has been observed in both overshadowing and blocking experiments that have been conducted with human and non-human animals, and that have used a variety of different landmarks and boundary shapes. Such results are consistent with the predictions made by the geometric module hypothesis (Cheng, 1986; Gallistel, 1990; Wang & Spelke, 2002, 2003), and also with the notion that the boundary shape of an environment is processed separately from landmarks, and learned about in a manner inconsistent with standard associative learning theories (Doeller & Burgess, 2008).

1.4 Evidence that shape is not special

Despite the abundance of observations that landmarks are unable to interfere with learning about the boundary shape of an environment, a number of recent experiments have found contradictory results. That is, landmarks have now been observed to both overshadow, and block, learning about the boundary shape of an environment. For example, in an overshadowing experiment by Pearce et al. (2006), an experimental group of rats was trained to find a goal that was hidden in one corner of a rectangle-shaped arena consisting of two long black walls and two short white walls. Relying on the geometry or the wall colours of each corner would lead the rats to the correct, or the geometrically equivalent, corner of the rectangle. For a control group the colour of the short and long walls changed, randomly, between trials. Consequently, rats could rely only on the geometry of the environment to navigate to the correct, or geometrically equivalent, corner. In a test trial conducted in an all-white rectangle, without the platform present, the control group spent significantly longer than the overshadowing group searching in the correct or geometrically equivalent corners. The clear implication of this result is that, for rats in the experimental group, learning about the boundary shape of the environment was overshadowed by the presence of landmarks that predicted the goal location, an effect that has been demonstrated in other studies conducted with rats (Cole, Gibson, Pollack, & Yates, 2011; Horne et al., 2010; Horne & Pearce, 2011; Kosaki, Austen, & McGregor, 2013), and experiments conducted with mountain chickadees (Gray, Bloomfield, Ferrey, Spetch, & Sturdy, 2005).

Recent experiments conducted with humans have also demonstrated that landmarks are able to overshadow learning about the boundary shape of a virtual environment. Redhead, Hamilton, Parker, Chan, and Allison (2013) trained participants in an overshadowing group to navigate to a goal that was located in a trapezium-shaped environment that contained two distinctive landmarks, one in each of the corners at the end of the longest wall. The goal was also located in one of the corners at the end of the longest wall and, thus, its location was signalled by both the unique geometry of the corner and the distinctive landmark within that corner. Participants in a control group received similar training; however, the landmarks presented to this group were identical. Consequently, the location of the goal was signalled only by the unique geometry of the corner in which it was placed. Following training, both groups received test trials in which the landmarks and goal were removed from the environment, and it was observed that the overshadowing group spent significantly less time searching in the corner of the trapezium that had contained the goal, relative to the control group. Clearly, then, the presence of a predictive landmark restricted participants learning about the location of a hidden goal with reference to the boundary shape of the environment. In the interest of completeness, it is important to acknowledge such an overshadowing effect did not occur when Redhead et al. (2013) trained an additional overshadowing and control group in an identical manner, save for the fact participants navigated in an isosceles triangle-shaped arena. During a test conducted in an empty isosceles triangular-shaped arena, participants in these groups spent an equivalent amount of time searching in the corner of the environment that had signalled the goal location. Nevertheless, consistent with the predictions of standard associative theories, the results observed in a trapezium-shaped environment suggest that the presence of landmarks can interfere with learning about the boundary shape of an environment, at least under some circumstances.

The results of some reorientation studies conducted with children have also been consistent with associative learning theories. For instance, Learmonth, Newcombe, and Huttenlocher (2001) replicated the experiment of Hermer and Spelke (1996), but in a 2.44 x 3.66 metre rectangle-shaped space. To recap, Hermer and Spelke asked children to locate a hidden toy in a 1.22 x 1.91 metre rectangle-shaped arena built from three white walls and one blue wall, and observed that children relied on the ambiguous geometry of the arena rather than an unambiguous blue wall to find the hidden toy. In the larger space used by Learmonth et al. (2001), however, children were able to use to the polarising blue wall to locate the hidden object, a result that been replicated in other studies conducted with children (Hupback & Nadel, 2005; Learmonth, Nadel, & Newcombe, 2002; Learmonth, Newcombe, Sheridan, & Jones, 2008; Newcombe, Ratliff, Shallcross, & Tywman, 2010), as well as fish (Sovrano, Bisazza, & Vallortigara, 2002), and rhesus monkeys (Gouteux, Thinus-Blanc, & Vauclair, 2001). In addition, it has been demonstrated that children are able to learn the location of a hidden goal placed at one end of a yellow polarising wall in a 1.22 x 1.91 metre rectangle-shaped arena when given pre-training in which a hidden goal was located in the centre of a yellow wall that comprised part of an equilateral triangular arena (Twyman, Freidman, & Spetch, 2007). In all of these examples, organisms have been observed to learn about more predictive landmark cue, at the expense of the less predictive information provided by the boundary shape of the environment. Such observations are entirely consistent with the predictions of associative theories of spatial navigation; however, it must again be acknowledged that, without an appropriate control condition in which organisms are required to learn only about the shape of the environment, it is difficult to determine whether these studies detected an overshadowing effect.

In addition to overshadowing, landmarks have also been observed to block learning about the boundary shape of an environment. Pearce et al. (2006) conducted a blocking experiment in which rats were first placed in a square arena comprising two adjacent black walls and two adjacent white walls, and were required to find a hidden platform in the corner where the two black walls joined. For rats in an experimental group, the platform was located at corner that was formed by two black walls whereas, for control rats, the platform was located at a corner formed by two white walls (see Figure 1.3). Following this initial training, rats were placed into a rectangle-shaped arena that also comprised two adjacent black walls and two adjacent white walls, and were again required to swim to a submerged platform. For rats in both groups, the platform was located in a corner formed by two black walls where, say, a short wall to the left of a long wall (see Figure 1.3 also).

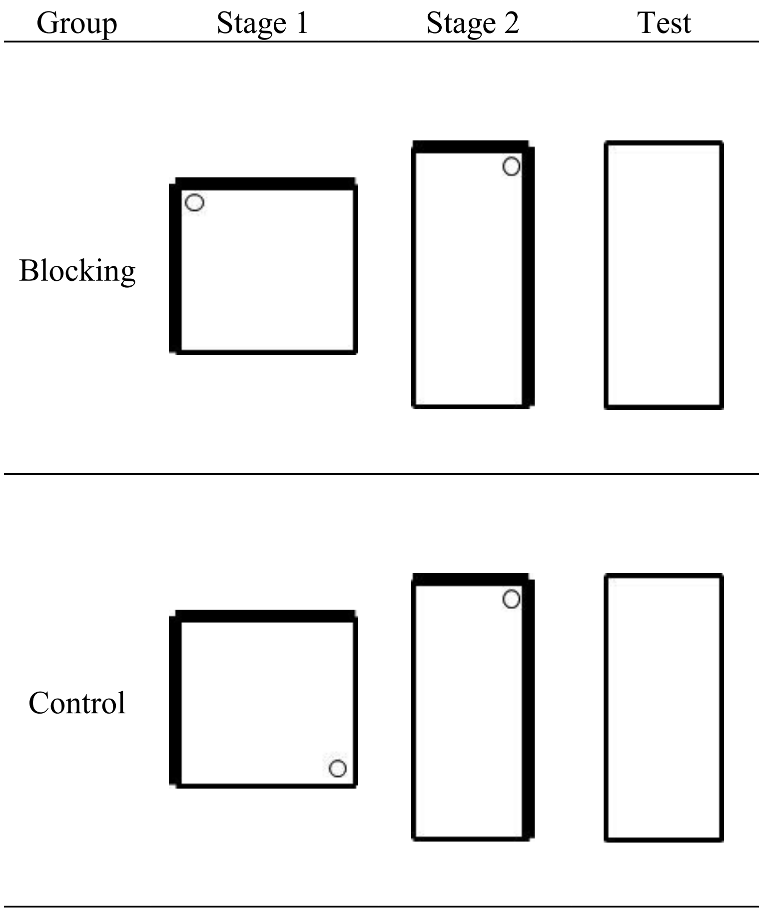


Figure 1.3. Design of the blocking experiment conducted by Pearce et al. (2006). White circles represent a submerged platform.

During a test trial conducted in extinction, rats were placed into rectangle-shaped arena, the walls of which were all the same colour. Whilst the rats in the control group displayed a significant preference for the corners of the rectangle where a short wall was to the left of a long wall, rats in the experimental group displayed no preference for any corner. These results, then, show a clear blocking effect in the experimental group, as learning about the wall colours in stage 1 prevented learning about the boundary shape of the rectangle in stage 2 (see also: Horne & Pearce, 2009a).

Similar observations of landmarks blocking learning about boundary shape have been observed in studies conducted with human participants, also. In stage 1 of an experiment conducted by Wilson and Alexander (2008), participants in a blocking group were placed into a circular virtual environment, and required to find a hidden goal that was located at a fixed vector relative to an intramaze landmark. In stage 2 of the experiment, participants were placed into an irregular trapezium-shaped arena that contained the same landmark that was present in stage 1. Participants were, again, required to locate a hidden goal that was located at the same fixed vector relative to an intramaze landmark as in stage 1 training. Participants in a control group received identical stage 2 training, however, in stage 1 control participants were asked to explore an unrelated maze of corridors. Following stage 2 training, test trials conducted in the same trapezium-shaped environment, but with the intramaze landmark removed, revealed that the control group took less time to locate the hidden goal compared to the blocking group. Consistent with the findings reported by Pearce et al. (2006), then, learning the location of the hidden goal with respect to an intramaze landmark prevented participants in the blocking group from learning the location of the hidden goal with respect to the boundary shape of the environment (see also Wilson & Alexander, 2010).

The experiments reviewed in sections 1.3 and 1.4 are summarised in Tables 1.1-1.4. Experiments in which a landmark has failed to overshadow (see Table 1.1), or block (see Table 1.3), learning about the boundaries of an environment are consistent with the idea that learning about the boundary shape of an environment occurs in a manner that is impervious to the influence of other cues, such as landmarks (e.g. Cheng, 1986; Doeller & Burgess, 2008; Gallistel, 1990; Wang & Spelke, 2002, 2003). Whilst demonstrations of landmarks failing to interfere with learning about the boundary shape of an environment are widespread, it is important to note experiments in which landmarks have overshadowed (see Table 1.2), or blocked (see Table 1.4), learning about the boundaries of an environment are particularly problematic for theories that afford the boundaries of an environment a special status during learning. In order to be consistent with the predictions of the geometric module (Cheng, 1986; Gallistel, 1990; Wang & Spelke, 2002, 2003), a landmark must *never* overshadow, or block, learning about the boundary shape of an environment. Similarly, circumstances in which landmarks have interfered with learning about the boundary shape of an environment are not consistent with proposals that animals learn about the boundary shape of an environment in a manner inconsistent with associative learning (Doeller & Burgess, 2008).

Table 1.1. Published experiments in which landmarks have failed to overshadow learning about information provided by the boundaries of an environment. From left-to-right, details about the species tested, authors, environments, landmarks, and boundary information are presented in separate columns. Asterisks indicate experiments in which learning to a compound of boundary and landmark information was compared to learning in a control group that learned only about boundary information.

Species	Authors	Environment	Landmarks	Boundary information
Children	Bullens et al. (2010)	Laboratory	Intra-maze traffic cone.	Circle, distal room cues
Rats	Cheng (1986)	Dry-Maze	Distinct 2D panels in each corner	Rectangle-shaped walls
Adult humans	Doeller & Burgess (2008)*	Virtual	Intra-maze traffic cone	Circle, distal landmarks
Adult humans	Doeller et al. (2008)*	Virtual	Intra-maze traffic cone	Circle, distal landmarks
Mice	Fellini et al. (2006)	Water-Maze	Black and white panel on short wall	Rectangle-shaped walls
Rats	Graham et al. (2006)*	Water-Maze	Black, and white, walls	Kite-shape walls
Rats	Hayward et al. (2003)*	Water-Maze	Sphere	Rectangle-shaped walls
Rats	Hayward et al. (2003)*	Water-Maze	Distal room cues	Triangle-shaped walls
Rats	Hayward et al. (2004)*	Water-Maze	White and black sphere	Rectangle-shaped walls
Children	Hermer & Spelke (1994)	Laboratory	Blue short wall	Rectangle-shaped walls
Children	Hermer & Spelke (1996)	Laboratory	Blue short wall	Rectangle-shaped walls
Children	Hermer-Vazquez et al. (2001)	Laboratory	Blue short wall	Rectangle-shaped walls
Pigeons	Kelly et al. (1998)*	Dry-Maze	Distinct 3D objects in each corner	Rectangle-shaped walls
Pigeons	Kelly et al. (1998)*	Dry-Maze	Distinct 2D panels in each corner	Rectangle-shaped walls
Rats	Margules & Gallistel (1988)	Dry-Maze	Distinct 2D panels in each corner	Rectangle-shaped walls
Rats	McGregor et al. (2009)*	Water-Maze	Black foam ball	Triangle-shaped walls
Rats	Pearce et al. (2001)*	Water-Maze	White disc attached to a black rod	Triangle-shaped walls
Adult humans	Redhead & Hamilton (2007)*	Virtual	Visible black, and white, platforms	Triangle-shaped walls
Fish	Sovrano et al. (2003)	Water-Tank	Distinct 2D panels in each corner	Rectangle-shaped walls
Chicks	Vallortigara et al. (1990)	Dry-Maze	Distinct 2D panels in each corner	Rectangle-shaped walls
Fish	Vargas et al. (2004)	Water-Tank	Grey and white striped walls	Rectangle-shaped walls
Children	Wang et al. (1999)	Laboratory	Red wall	Square-shaped walls

Table 1.2. Published experiments in which landmarks have overshadowed learning about information provided by the boundaries of an environment. From left-to-right, details about the species tested, authors, environments, landmarks, and boundary information are presented in separate columns. Asterisks indicate experiments in which learning to a compound of boundary and landmark information was compared to learning in a control group that learned only about boundary information.

Species	Authors	Environment	Landmarks	Boundary information
Rats	Cole et al. (2011)*	Dry-Maze	Black, white, and stripped walls	Kite-shaped walls
Chickadees	Gray et al. (2005)*	Dry-Maze	Single blue wall, long or short	Rectangle-shaped walls
Rhesus Monkeys	Gouteux et al. (2001)	Chamber	Blue, or chequered, short wall	Rectangle-shaped walls
Rats	Horne et al. (2010)*	Water-Maze	Camping lantern	Circle, distal room cues
Rats	Horne & Pearce (2011)*	Water-Maze	Black or white A4 cards	Rectangle-shaped walls
Children	Hupback & Nadel (2005)	Laboratory	Yellow wall	Rhombus-shaped walls
Rats	Kosaki et al. (2013)*	Water-Maze	Black tennis ball	Rhombus-shaped walls
Children	Learmonth et al. (2001)	Laboratory	Bookshelf and door	Rectangle-shaped walls
Children	Learmonth et al. (2002)	Laboratory	Blue short wall	Rectangle-shaped walls
Children	Learmonth et al. (2008)	Laboratory	Red short wall	Rectangle-shaped walls
Children	Newcombe et al. (2010)	Laboratory	Single red wall	Octagon-shaped walls
Rats	Pearce et al. (2006)*	Water-Maze	Black, and white, walls	Rectangle-shaped walls
Adult humans	Redhead et al. (2013)*	Virtual	Black cube	Trapezium-shaped walls
Fish	Sovrano et al. (2002)	Water-Tank	Blue short wall	Rectangle-shaped walls
Children	Twyman et al. (2007)	Laboratory	Yellow wall	Rectangle-shaped walls

Table 1.3. Published experiments in which landmarks have failed to block learning about information provided by the boundaries of an environment. From left-to-right, details about the species tested, authors, and environments are presented in separate columns. The 2 right-most columns present details about the landmark that signalled the goal location in stage 1 of the experiment, and details about the to-be-blocked boundary information in stage 2 of the experiment. Subscript letters in the landmark column indicate the shape created by the walls of the arena that contained the landmark in stage 1: c = circle, n = no walls r = rectangle, s = square, t = triangle.

Species	Authors	Environment	Landmarks	Boundary information
Adult humans	Doeller & Burgess (2008)	Virtual	Traffic cone, distal landmarks ^{n}	Circle, distal landmarks
Adult humans	Doeller et al. (2008)	Virtual	Traffic cone, distal landmarks ^{n}	Circle, distal landmarks
Rats	Hayward et al. (2003)	Water-Maze	Sphere ^{r}	Triangle-shaped walls
Rats	Hayward et al. (2004)	Water-Maze	White and black sphere ^{r}	Triangle-shaped walls
Rats	Hayward et al. (2004)	Water-Maze	White and black sphere ^{t}	Rectangle-shaped walls
Rats	Pearce et al. (2001)	Water-Maze	White disc attached to a black rod ^{c}	Triangle-shaped walls
Adult humans	Redhead & Hamilton (2009)	Virtual	Visible black, and white, platforms ^{c}	Triangle-shaped walls
Rats	Wall et al. (2004)	Dry-Maze	Black plastic corner panel ^{s}	Rectangle-shaped walls

Table 1.4. Published experiments in which landmarks have blocked learning about information provided by the boundaries of an environment. From left-to-right, details about the species tested, authors, and environments are presented in separate columns. The 2 right-most columns present details about the landmark that signalled the goal location in stage 1 of the experiment, and details about the to-be-blocked boundary information in stage 2 of the experiment. Subscript letters in the landmark column indicate the shape created by the walls of the arena that contained the landmark in stage 1: c = circle, s = square, t = triangle.

Species	Authors	Environment	Landmarks	Boundary information
Rats	Horne & Pearce (2009a)	Water-Maze	Black sphere ^{t}	Triangle-shaped walls
Rats	Horne & Pearce (2009a)	Water-Maze	Black sphere ^{c}	Triangle-shaped walls
Rats	Pearce et al. (2006)	Water-Maze	Black and white walls ^{s}	Rectangle-shaped walls
Adult humans	Wilson & Alexander (2008)	Virtual	3D grey cross ^{c}	Trapezium-shaped walls
Adult humans	Wilson & Alexander (2010)	Virtual	3D cube, cross, and pyramid ^{c}	Circle, four colour walls

1.5 Global and local encoding of shape information

As reviewed previously, a number of theories predict that information provided by the boundary shape of the environment is learned about separately from landmarks (e.g. Cheng, 1986; Doeller & Burgess, 2008; Gallistel, 1990; Wang & Spelke, 2002, 2003), and there has been much debate as to whether, or not, learning about the boundary shape of an environment is prone to interference from landmark cues. More fundamentally, though, there has also been debate as to exactly how animals encode information provided by the boundary shape of the environment, regardless of the presence of other cues such as landmarks. The focus of this debate has been whether animals use a global- or a local-shape representation when navigating within an environment.

As seen earlier, rats trained to find buried food in the corner of a rectangle-shaped arena learn about the ambiguous geometric cues that signal the goal location in circumstances where an unambiguous landmark is located in each corner (Cheng, 1986). On the basis of these results, Cheng proposed that shape information provided by the boundary walls of an environment is processed in a dedicated geometric module, which supports encoding of only a global representation of the shape properties of an environment (See also: Wang & Spelke, 2002, 2003). A similar conclusion was also reached by Cheng and Spetch (1998) who, when discussing the findings reported by Cheng (1986), claimed that the animals were using only the broad shape of the environment to find the buried food. Similarly, in the context of discussing Cheng's work, Gallistel (1990) claimed that animals navigate on the basis cognitive maps that represent only the Euclidean shape of the environment. The notion that animals encode a global representation of the shape of the environments they navigate in has not gone unchallenged, however. As noted by Pearce, Good, Jones, and McGregor (2004), it is possible to explain the findings reported by Cheng (1986) by assuming that, instead of encoding a global representation of the shape of the environment, rats learn the location of the buried food on the basis of local-shape information. According to this analysis, rats associate food with a more egocentrically defined representation of the geometry of the environment, such as the sight of a short wall is to the left of long wall. Crucially, the corner diametrically opposite this baited corner is geometrically identical and, thus, also has a short wall to the left of a long wall. Rats navigating on the basis of local-shape information, therefore, would also be expected to visit the diametrically opposite corner, as was observed in the experiments conducted by Cheng (1986: see also: Margules & Gallistel, 1988).

In a shape transformation experiment designed to assess if animals navigate on the basis of local-shape information, Pearce et al. (2004) trained rats to find a submerged platform in a right-angled corner of a kite-shaped environment. Once rats had learned to locate the platform, they were given test trials in a rectangle-shaped environment that was built from the same walls as the kite-shaped environment. Whilst the global shapes of these two environments were different, both the kite- and rectangle-shaped environments share some local-shape properties. Specifically, each arena contains at least one right angled corner where a short wall is to the left of a long wall, and at least one right angled corner where a short wall is the right of a long wall. If, during training, rats were using a representation of the global-shape of the kite to locate the goal, then this would be of little help in the rectangle-shaped test environment where the global-shape was now different. If, however, the rats were using the local-shape properties of the kite-shaped environment to locate the goal, then the rats should preferentially search in the corner of the rectangle that shares these local-shape properties. Pearce et al. (2004) observed that rats searched in the corner of the rectangle-shaped arena that shared the same local-shape properties that signalled the goal location in the kite-shaped environment, a result which appears inconsistent with accounts of spatial learning that emphasise global-shape learning. Similar search preferences have been replicated in spontaneous object recognition paradigms (Poulter, Kosaki, Easton, & McGregor, 2013), using landmark arrays (Esber, McGregor, Good, Hayward, & Pearce, 2005), and in experiments conducted with adult humans (Lew et al., 2014). In addition, experiments conducted with chicks (Tommasi & Polli, 2004), and humans (Lubyk, Dupuis, Gutierrez, & Spetch, 2012), have demonstrated that navigational behaviour that is based on the lengths and angles of a parallelogram-shaped environment transferred to both rectangle- and rhombus-shaped environments, respectively.

It is important to note that, although the results above appear inconsistent with theories that suggest animals navigate based on the global-shape of an environment, evidence that animals encode the local-shape properties of an environment whilst navigating does not constitute evidence against the encoding of global-shape properties. For instance, in the first stage of the experiment conducted by Pearce et al. (2004), it is possible that animals encoded *both* the local- and global-shape properties of the kite-shaped environment. At test, however, the global representation of the kite-shaped training environment would be incongruent to the, now, rectangle-shaped test arena. Consequently, any global representation encoded by rats during training would be of little worth in guiding navigation during test, thus, forcing rats to navigate on the basis of the local-shape properties that were preserved between the training and testing environments. In a comment on shape transformation studies conducted by Pearce et al. (2004) and Tommasi and Polli (2004), Cheng and Gallistel (2005) argued that the results of the experiments could, in fact, be explained by a global-shape property of the environment, namely, the principal axis. The principal axis is colloquially known as the long axis, and passes through the centre of any shape (see Cheng, 2005). In a rectangle, the principal axis connects the centre of each short wall and, in a kite, it runs from the acute corner to the obtuse corner. Cheng and Gallistel (2005) suggested that, during navigation, animals extract the principal axis of the shape of the environment they are navigating, and align a global representation of the Euclidean shapes of environments using this axis. The behaviour of rats in the experiment conducted by Pearce et al. (2004), for example, could be explained if animals navigated to the corner that was the furthest to the right of the principal axis in both training and test arenas. In both a rectangle- and kite-shaped environment, navigating to the furthest wall to the right of the principal axis would lead the animal to the corners which shared the same local geometry of a short wall to the left of a long wall.

Evidence that organisms navigate on the basis of the principal axes of shapes is somewhat ambiguous. In an experiment conducted by McGregor, Jones, Good, and Pearce (2006), rats were first trained to find a hidden goal in an irregular pentagon-shaped arena (see Figure 1.4). The goal was located in a right-angled corner where a short wall was to the right of a long wall and, importantly, this corner was on the right side of the principal axis. In a test trial, rats were allowed to swim, for 60 seconds, in a rectangle-shaped arena which contained no hidden goal. During this test, rats preferentially searched in corners where a short wall was to the right of a long wall which, crucially, are on the left side of the principal axis. Whilst this result shows that, when placed in conflict, rats preferentially navigate using local geometric cues over the principal axis (See also: Kelly, Chiandetti, & Vallortigara, 2010), it does not rule out the possibility that rats are able to navigate on the basis on the principal axis.

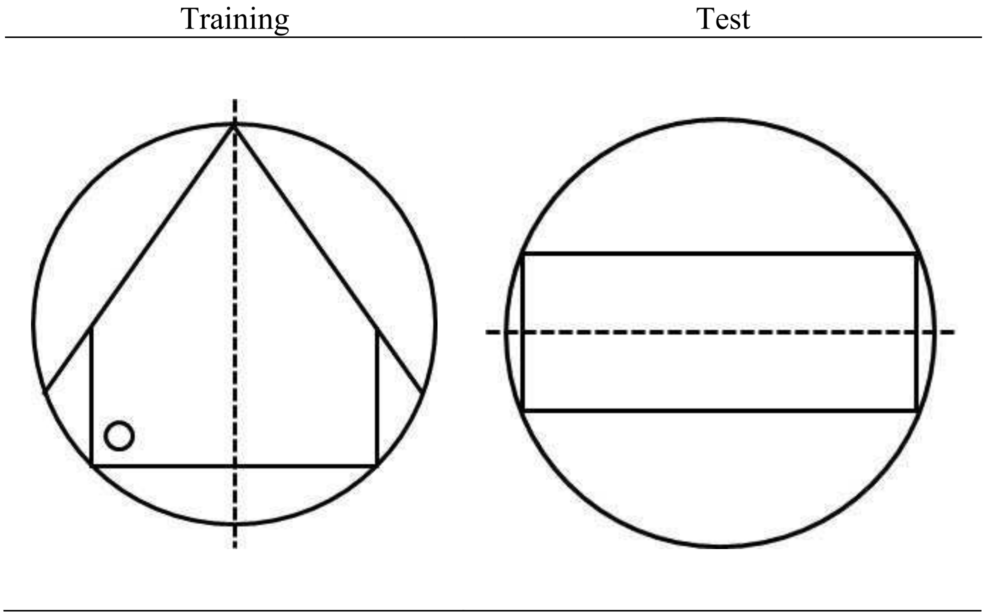


Figure 1.4. Design of the shape transformation experiment conducted by McGregor et al. (2006). The white circle represents the location of the submerged platform. The dotted lines that are superimposed on each environment indicate the principal axis of each shape.

A similar preference for navigating on the basis of local geometric cues over the principal axis, when the two are placed into conflict, has been observed in adult humans. For example, Bodily, Eastman, and Sturz (2011) trained participants, in a trapezium-shaped environment that comprised three equally sized short walls and one long wall, to find a goal located at the obtuse corner that was on the right side of a principal axis. Participants were then placed into a parallelogram-shaped environment where the obtuse corners were located on the left side of the principal axis. In keeping with the results reported by McGregor et al. (2006), participants preferentially searched in the obtuse corners of the parallelogram and, thus, on the opposite of the trained side of the principal axis. Bodily et al. (2011) also administered test trials in a rectangle-shaped environment and, here, participants preferentially searched in the corners of the rectangle where a short wall was to the left of a long wall. The authors argued that, because the walls either side of the goal location in the trapezium were the same size, and because there were no obtuse corners in the rectangle-shaped test arena, local-shape information could not have been driving this behaviour. Instead, it was suggested that the preference shown by participants in the rectangle-shaped arena was driven by them navigating to corners that were on the right side of the principal axis, as it was this side of the principal axis that was rewarded during training (See also: Sturz & Bodily, 2011; Sturz, Forloine, & Bodily, 2012; Sturz, Gurley, & Bodily, 2011; Sturz, Kilday, & Bodily, 2013).

To summarise the evidence reviewed above, it has been demonstrated that, under appropriate conditions, animals can navigate on the basis of the local-shape properties provided by the boundary walls of an environment (e.g.

McGregor et al., 2006). Animals can also preferentially navigate on the basis of the local-shape properties in circumstances where the location signalled by previously rewarded local-shape properties, and the location signalled by the previously rewarded side of the principal axis, are placed into conflict. In environments where these previously rewarded local-shape properties are no longer present, animals have been observed to navigate to the previously rewarded side of the principal axis (Bodily et al., 2011).

1.6 The Miller-Shettleworth model

The experiments reviewed in section 1.5 provide evidence that it might be possible to explain navigational behaviour by assuming that animals navigate only on the basis of the local-shape properties of an environment. There was, however, some evidence that animals navigate on the basis of the principal axis of an environment. The experiments reviewed in the sections 1.3 and 1.4 provide conflicting evidence. Under some circumstances, landmarks failed to interfere with learning about the boundary shape of an environment. Under other circumstances, learning about the boundary shape of an environment was overshadowed, or blocked, by learning about landmark cues. As noted previously, these latter findings are particularly problematic for theories that suggest learning about the boundary shape of an environment occurs in a manner that is impervious to the influence of landmarks (e.g. Cheng, 1986; Doeller & Burgess, 2008; Gallistel, 1990). In contrast, given that overshadowing and blocking are hallmark effects of associative learning, observations of a landmark restricting, or preventing, learning about the boundary shape of an environment are entirely consistent with standard associative learning theories (e.g. Mackintosh, 1975; Pearce & Hall, 1980; Rescorla & Wagner, 1972). At first glance, however, instances in which a landmark has failed to overshadow, or block, learning about the boundary shape of an environment appear inconsistent with standard associative learning theories.

In order to provide a reconciliation of the discrepant cue competition findings (see Tables 1.1 to 1.4), Miller and Shettleworth (2007, 2008, 2013) suggested an associative analysis of spatial navigation in which geometric information is permitted to compete with landmark information. When describing the rationale for their model, Miller and Shettleworth (2007) noted that it is difficult to apply standard associative theories to spatial learning as, unlike Pavlovian conditioning experiments in which the experimenter can precisely control how stimuli are paired with a trial outcome, the behaviour of an animal in spatial experiments determines the manner in which it experiences stimuli-reward contingencies. By incorporating the probability that an animal navigates to a particular place of an environment on a given trial, the Miller-Shettleworth model ensures that only the stimuli that the animal experiences on a given trial change in associative strength. As will be described below, it is this part of the model that permits Miller and Shettleworth to explain the absence of cue competition effects in the spatial domain.

According to the Miller-Shettleworth model, navigational cues, which include landmarks and the shape information that is provided by the boundary walls of an environment, are encoded as representational elements. These elements compete for an association with a navigational goal according to a modification of the learning rule proposed by Rescorla and Wagner (1972) shown in Equation 1.

$$\Delta V_E = \alpha\ (\lambda - V_L)\ P_L \qquad \text{Equation 1.}$$

Here, V_E is the strength of the association between a representational element and the navigational goal, α is the inherent salience of that element, λ is the asymptote of learning supported by the navigational goal, and V_L is the sum of the associative strengths of all elements at a particular location. The addition of P_L to the Rescorla-Wagner model expresses the probability of choosing a particular location within an environment, which itself is defined as:

$$P_L = V_L / \Sigma V_L \qquad \text{Equation 2.}$$

As before, V_L is the associative strength of all elements at a particular location, and ΣV_L in Equation 2 is the sum of the associative strengths of all locations. The addition of P_L to the Rescorla-Wagner model allows the model proposed by Miller and Shettleworth to predict that the presence of a landmark will, sometimes, overshadow learning about the boundary shape of an environment and, other times, will not. The Miller-Shettleworth model explains instances in which a landmark successfully restricts learning about the boundary shape of an environment in a similar manner to the Rescorla-Wagner model. That is, the elements representing the landmark and corner geometry compete with each other for a limited amount of associative strength to the navigational goal, such that the associative strength of each element is weaker than if either cue was trained in isolation. This overshadowing process can, however, be undermined by a process Miller and Shettleworth (2007) termed feature enhancement. Consider the case in which a navigational goal is located in one corner of a rectangle-shaped arena that contains no landmarks. Equation 1 permits that an association will form between the geometric elements of the correct corner and the navigational goal. This learning will progress relatively slowly, though, as the geometrically equivalent corner of the rectangle will also be visited. As the goal is not present in this corner, such visits will weaken the association between these elements and the goal. Now consider a basic overshadowing design, in which a navigational goal is again located in one corner of a rectangle-shaped arena, but also placed within that corner is a distinctive landmark. Equation 1 ensures that the association between the geometric elements within the correct corner and the navigational goal will increase and, correspondingly, so too will the probability of visiting this corner. The geometrically equivalent corner, however, is not identical to the correct corner as it does not contain the landmark. This corner, therefore, will not be visited as frequently as in the previous example. Consequently, the elements shared by the correct and geometrically equivalent corners will tend to gain, *but not lose*, associative strength. Relative to a control group, therefore, the presence of a landmark might actually serve to enhance learning about the geometry of an environment, thus, undermining the overshadowing effect. It should be noted that this feature enhancement occurs early in training, and the Miller-Shettleworth model anticipates an overshadowing effect would eventually be observed after sufficient training.

The addition of P_L to the Rescorla-Wagner model also allows the model proposed by Miller and Shettleworth to predict that a landmark will sometimes block learning about the boundary shape of an environment and, other times, will not. Consider an experiment in which an animal is initially trained to locate a navigational goal on the basis of only a landmark cue, after which it is placed into a novel arena in which the goal can be located on the basis of the boundary shape of the environment, as well as the original landmark cue. The presence of the predictive landmark cue in stage 2 will ensure that the animal continues to approach it; however, in doing so, it is also exposed to the geometric cues that signal the goal location in stage 2. As with overshadowing effect, the Miller-Shettleworth model explains instances in which a landmark successfully blocks learning about the boundary shape of an environment in the same manner as the Rescorla-Wagner model. Here, the associative strength of the landmark elements which signal the goal location in stage 1 approach asymptote and, thus, prevent the representational elements of the geometric cues gaining associative strength when they are introduced in stage 2. Instances in which landmarks fail to block learning about the boundary shape of an environment are, again, explained by the Miller-Shettleworth model through feature enhancement. During stage 1 training, the probability choice rule described in Equation 2 ensures that the animal consistently approaches the landmark that signals the goal location long before the associative strength of the landmark reaches asymptote. Consequently, at the onset of stage 2, as the animal consistently approaches the landmark cue, the associative strength of the correct geometry to which it is also exposed increases quicker than would normally be expected. This follows because, at the outset of stage 2, the associative strength of the goal location will be higher than the associative strength of any other location in the arena, ensuring that the probability of visiting the goal location will be greatest, even if learning about the landmark cue in stage 1 might have been incomplete. Relative to an appropriate control group, therefore, learning about environmental geometry would appear unimpaired in the blocking group. Like overshadowing experiments, though, feature enhancement occurs only in circumstances where minimal training is given in stage 1 during blocking experiments and, following sufficient training in stage 1, the Miller-Shettleworth model anticipates a blocking effect.

Despite providing an elegant explanation as to why, under some circumstances, landmarks are successful and, in other circumstances, unsuccessful in interfering with learning about the boundary shape of an environment, there are short comings to the model proposed by Miller and Shettleworth (2007, 2008, 2013). For example, an experiment conducted by McGregor et al. (2009) demonstrated that the Miller-Shettleworth model does not accurately predict all spatial behaviour (see also Horne & Pearce, 2010). In their experiment, McGregor et al. (2009) trained rats to swim to a submerged platform that was located in one of the corners at the end of the shortest wall of a triangular-shaped arena. For rats in an overshadowing group, a black spherical landmark was suspended above the platform location. For overshadowing rats, therefore, the location of the platform was signalled by both the geometry of the arena and the landmark cue. Rats in a control received similar training; however, a second black spherical landmark was present in the corner at the end of the shortest wall of the arena that did not contain the platform. Consequently, for control rats, only the geometry of the pool signalled the goal location. McGregor et al. (2009) reported computer simulations of the Miller-Shettleworth model which demonstrated that the model predicts that the landmark in the overshadowing group will overshadow learning about the geometry of the arena, relative to learning about the geometry of the arena in the control group. To test this prediction, rats were allowed to swim in the triangular pool, in the absence of the landmark and platform, for 60 seconds. During this test trial, rats in the overshadowing group spent an equivalent amount of time searching in the corner of the pool that had previously contained the platform, compared to rats in the control group. Contrary to the prediction of the Miller-Shettleworth model, then, the predictive landmark cue did not restrict learning about the geometry of the pool in the overshadowing group.

1.7 Structure of the thesis

Whilst the experiment conducted by McGregor et al. (2009) demonstrates that the predictions of the Miller-Shettleworth model are not always observed, the experiment was not designed to assess the underlying psychological mechanisms proposed in the Miller-Shettleworth model. The experiments reported in this thesis were designed to test three key predictions that can be derived from the Miller-Shettleworth model. First, Miller and Shettleworth proposed that elemental geometric cues compete with other elemental non-geometric cues for an association with a navigational goal. Consequently, the model predicts that blocking should be present if the global-shape of the environment is changed, but the elemental geometric cues are preserved. The experiments reported in Chapter 2 tested this prediction. Second, as a consequence of using the Rescorla-Wagner theory as its starting point for learning, the model proposed by Miller and Shettleworth (2007, 2008, 2013) inherits the assumption that the associability of a navigational stimulus (or stimulus dimension) is fixed. Consequently, the model predicts that the salience of cues within the environment is not modifiable (cf. Mackintosh, 1975). Theories that propose that learning about the shape of the environment is governed by a global representation (e.g. Cheng, 1986; Gallistel, 1990) are similarly silent about the possibility that the salience of geometric information or navigational cues might be modifiable. The experiments reported in Chapter 3 and 4 assessed whether the salience of spatial cues is modifiable. Third, according to Miller and Shettleworth (2007, 2008, 2013), changes in associative strength are permitted for elements at an individual corner, rather than for all locations together. Consequently, the model does not advance the possibility of learning taking place to a representation of the global-shape of the environment. The experiments reported in Chapter 5 assessed if humans encode a representation of the global-shape of the environments in which they navigate.

Chapter 2

Blocking spatial navigation across environments that have a different shape

There is considerable evidence to suggest that navigation that is based upon landmarks is consistent with an associative explanation for spatial learning (e.g. Chamizo et al., 2003; Chamizo et al., 2006; Gould-Beierle & Kamil, 1999; Leising et al., 2011, 2014; Redhead et al., 1997; Roberts & Pearce 1999; Rodrigo et al., 1997, 2005; Sanchez-Moreno et al., 1999; Stahlman & Blaisdell, 2009). There remains, however, a debate as to whether learning about the boundary shape of an environment progresses according to the same associative principles. Observations that rats (e.g. Cheng, 1986; Margules & Gallistel, 1988), and humans (Redhead & Hamilton, 2007), learn the location of a reward with respect to the ambiguous geometric cues of a rectangle-shaped arena, despite the presence of landmarks which unambiguously signal the reward location, have led to the suggestion that organisms encode a global representation of the shape of their environments in a dedicated geometric module that is impervious to the influence of non-geometric cues (Cheng, 1986; Gallistel, 1990; Wang & Spelke, 2002, 2003).

The suggestion that animals encode a global representation of the boundary shape of the environments in which they navigate has not gone unchallenged, however. Animals need not learn anything about the global-shape of an environment in order to find a reward located in, for example, one corner of a rectangle-shaped environment. Instead, animals could learn to navigate to a reward by approaching, say, a right-angled corner where the left wall was shorter than the right wall. This local explanation of spatial behaviour does not require animals to acquire any knowledge of the global-shape of the environment (Pearce et al., 2004), and evidence consistent with this account of navigation has been provided by a number of shape transformation experiments. Animals that are initially trained to locate a reward in one corner of a given shape preferentially search in a corner that shares the same local-shape cues when placed into a novel arena (Lew et al., 2014; McGregor et al., 2006; Pearce et al., 2004; Poulter et al., 2013; Tommasi & Polli, 2004). If animals navigate only on the basis of a global representation of the boundary shape of their environment, when placed into a novel shape, there would be no reason to observe a preference one corner over another.

As noted in Chapter 1, the associative model of spatial navigation proposed by Miller and Shettleworth (2007, 2008, 2013) suggests that the geometric cues that are provided by the boundary shape of an environment, and other cues such as landmarks, are encoded as elements. These elements are permitted to compete with each other for associative strength and, consequently, the Miller-Shettleworth model can successfully explain the results of a number of experiments where landmarks have successfully blocked learning about geometric information (e.g. Horne & Pearce, 2009a; Pearce et al., 2006; Wilson & Alexander, 2008). In these experiments, if it is assumed that animals learned about local geometric cues (e.g. Pearce et al., 2004), then it is learning about local geometric information that has been blocked by landmarks.

Despite observations that appear consistent with the proposal above, it is difficult to find evidence that supports the notion that local geometric information competes with other cues, such as landmarks. In stage 1 of the experiment conducted by Pearce et al. (2006), rats were placed in a square arena comprising two adjacent back walls and two adjacent white walls, and were required to find a hidden platform in the corner where the two black walls joined. Following this training, rats were placed into a rectangle-shaped arena that also comprised two adjacent black walls and two adjacent white walls, and were again required to swim to a submerged platform. For rats in an experimental group, the platform was located in the all-black corner which had a short wall to the left of a long wall. For rats in a control group, the platform was now located in the all-white corner that had a short wall to the left of the long wall. During a test conducted in extinction, rats were placed into a rectangle-shaped arena, the walls of which were all the same colour. Whilst the rats in the control group displayed a significant preference for the corners of the arena where a short wall was to the left of a long wall, rats in the experimental group displayed no preference for any corner. Consistent with the Miller-Shettleworth model, then, these results demonstrated a blocking effect. In the experimental group, learning about the wall colours in stage 1 prevented learning about the shape information in stage 2. As the test trials were conducted in an environment that was the same shape as the environment from stage 2 training, though, it is not clear whether learning about the wall colours in stage 1 of the experiment blocked learning about the local geometric cues of the environment in stage 2 or, instead, learning about the global-shape of the environment.

The experiments reported in Chapter 2 were designed to assess if learning about local geometric cues competes with learning about non-geometric cues, in a manner consistent with the Miller-Shettleworth model. The purpose of Experiment 1 was to, first, demonstrate that spatial learning that is based about the shape of one environment (e.g. a rectangle) transfers to a different-shaped environment (e.g. a kite), in order to provide a measure of navigation that is based upon the local geometric cues of that environment (see: Lew et al., 2014; McGregor et al., 2006; Pearce et al., 2004). In Experiments 2 and 3, the procedures from Experiment 1 were applied to blocking, and assessed if the geometric information that is transferred between environments that have a different shape can be blocked by (Experiment 2), or block (Experiment 3), learning about non-geometric wall colour cues. As the Miller-Shettleworth model applies no special status to geometric cues over non-geometric cues, the model anticipates a reciprocal blocking effect. That is, learning about coloured walls should both block, and be blocked by, learning about local geometric information. According to the geometric module hypothesis (Cheng, 1986; Gallistel, 1990), however, geometric and non-geometric information should not compete with each other for control over behaviour. Consequently, a blocking effect should not be observed in either Experiment 2 or 3. Finally, a different set of predictions can be generated from the model of navigation proposed by Doeller and Burgess (2008). According to this model, learning about landmark information is subject to cue competition effects; however, learning about environmental boundaries occurs in an incidental manner, such that it is immune to cue competition effects. Consequently, landmark information may be blocked by information provided by the boundary shape of an environment, but not vice versa. Assuming that wall colours provide landmark information, then, learning about wall colours should not block learning about boundary shape in Experiment 2. In contrast, learning about boundary shape in Experiment 3 should block learning about wall-colour information.

2.1 Experiment 1

The purpose of Experiment 1 was to establish parameters, in the Nottingham lab, with which learned spatial behaviour would transfer from a kite- to a rectangle-shaped arena, and vice versa. Half of the participants (group kite-rectangle) were trained to find a hidden goal in one of the right-angled corners of a kite-shaped arena. The remaining participants (group rectangle-kite) were trained to find the hidden goal in one of the corners of a rectangle-shaped arena. Following this training, participants were given two 60s test-trials conducted in the absence of the hidden goal in a kite-shaped arena for group rectangle-kite and in rectangle-shaped arena for group kite-rectangle. One test trial was conducted in an arena that had walls the same colour as the arena in which participants were trained. If participants transfer the local-shape information from the training to the test arena, then they should preferentially search in the corner(s) of the test arena that match the local geometric cues of the training arena (Lew et al., 2014; McGregor et al., 2006; Pearce et al., 2004). A second test trial was also conducted in which the walls were a different colour to the walls of the arena in which participants were trained. This test was designed to assess how susceptible to generalisation decrement the transfer of local-shape information is (see Graham et al., 2006), an effect that would require minimising in Experiments 2 and 3.

2.1.1 Method

2.1.1.1 Participants

32 participants were recruited from the University of Nottingham (26 female), and were given course credit in return for participation. The age of participants ranged from 18 to 33 years (mean = 21.72, *SD* = 5.00). A £10 prize was awarded to the participant who completed the experiment in the shortest time.

2.1.1.2 Materials

All virtual environments were constructed and displayed using Mazesuite software (Ayaz, Allen, Platek, & Onaral, 2008; www.mazesuite.com), using a standard Stone desktop computer, running Microsoft Windows 7. A large Mitsubishi LDT422V LCD screen (935 x 527 mm) was used to display the virtual environments. All virtual arenas were viewed from a first-person perspective, and a grass texture was applied to the floor of each arena. Using the 0-255 RGB scale employed by Mazesuite, the cream-coloured walls used in the experiment were defined as 204, 178, 127, and the blue-coloured walls were defined as 178, 204, 229.

Assuming a walking speed similar to that in the real world (2 m/s), the perimeter of both the kite- and rectangle-shaped arenas was 72m, with the small walls being 9m, and the long walls 27m, in length. The height of the walls in both arenas was approximately 2.5 m. The kite-shaped arena contained two right-angled corners, with the remaining two angles being 143.14° and 36.86°. The rectangle-shaped arena, by definition, contained four right-angled corners. Finally, the goals within all arenas were square-shaped regions (1.08m x 1.08m, invisible to participants), the centre of which was always located 2.48m away from the walls of the arena, along on a notional line that bisected a right-angled corner.

A third arena was also used in this experiment, which was designed to allow participants to become familiar with the controls of the experimental task. This exploration arena was a regular octagon configured with red walls (RGB: 229, 25, 51), with a grass texture again applied to the floor. There was no hidden goal present. Again assuming a walking speed of 2 m/s, each wall of the exploration arena was 12m in length.

2.1.1.3 Procedure

General. After signing a standard consent form, participants were given the following set of instructions on paper:

This study is assessing human navigation using a computer generated virtual environment. During this experiment, you will complete 20 trials. In each trial, you will be placed into a room that contains an invisible column. Your aim is to end the trials as quickly as possible by walking into the column.

You will view the environment from a first person perspective, and be able to walk into the column from any direction using the cursor keys on the keyboard. Once you've found the column a congratulatory message will be displayed and you should hit enter when you're ready to begin the next trial. You will always be in the centre of the arena when a trial begins, but the direction in which you face at the start of each trial will change.

To start with, you may find the column is difficult to find. The column does not move though, so it is possible to learn its specific location as the experiment goes along. It's a good idea to fully explore the environment on the first few trials to become aware of your surroundings. This should help you in learning where the hidden column is.

This session should take around 15 minutes. If at any point you wish to stop this session, please notify the experimenter and you'll be free to leave without having to give a reason why. Your results will be saved under an anonymous code, and kept confidential throughout.

The person who takes the least time to complete this experiment will win a £10 prize!

Participants sat not more than 100 cm from the screen, and were first provided with the opportunity to move around the octagonal exploration arena for two 30 second trials using the four keyboard cursor keys. Presses on the "up" and "down" cursor keys permitted the participant to move forwards and backwards within the arena, respectively. Presses on the "left" and "right" cursor keys permitted the participant to rotate, respectively, counter-clockwise and clockwise within the arena. Following these exploration trials, participants completed the acquisition trials, in which they were required to find the hidden goal by using the four cursor keys as described previously. There was no time limit imposed on any trials which contained a hidden goal, thus, such trials ended only when participants found the hidden goal. Once the hidden goal was found, participants could no longer move, and a congratulatory message (*Congratulations, you found the goal!*) was displayed on screen. Participants pressed enter to begin the next trial. In the kite-shaped arena, participants always began each trial at a point located halfway between the apex and obtuse corners and, in the rectangle-shaped arena, participants began each trial in the centre of the arena. The direction in which participants faced at the onset of each trial was randomised in the both kite- and rectangle-shaped arenas.

Acquisition. Sixteen participants received acquisition trials in a kite-shaped arena. For 8 of these participants, the hidden goal was located in the right-angled corner where a short wall was to the left of a long wall (corner A - see Figure 2.1) whereas, for the other 8 participants, the goal was located in the right-angled corner where a long wall was to the left of a short wall (corner C – see Figure 2.1). When the goal was located in the corner where the short wall was to the left of the long wall, the whole arena was blue for 4 participants, and for the other 4 participants the arena was cream (see Figure 2.2). This was also true for when the goal was in the corner where the long wall was to the left of a short wall. The remaining sixteen participants received acquisition trials in a rectangle-shaped arena. The location of the hidden goal and the colour of the walls were counterbalanced in the same manner as described for the kite-shaped arena. To ensure that visits to the correct corners of the rectangle were always rewarded, each rectangle-shaped arena contained two goal locations. When the goal was located in a right-angled corner where a short wall was to the left of a long wall, hidden goals were present in corners W and Z. Similarly, when the goal was located where a long wall was to the left of a short wall, hidden goals were present in corners X and Y (see Figure 2.1).

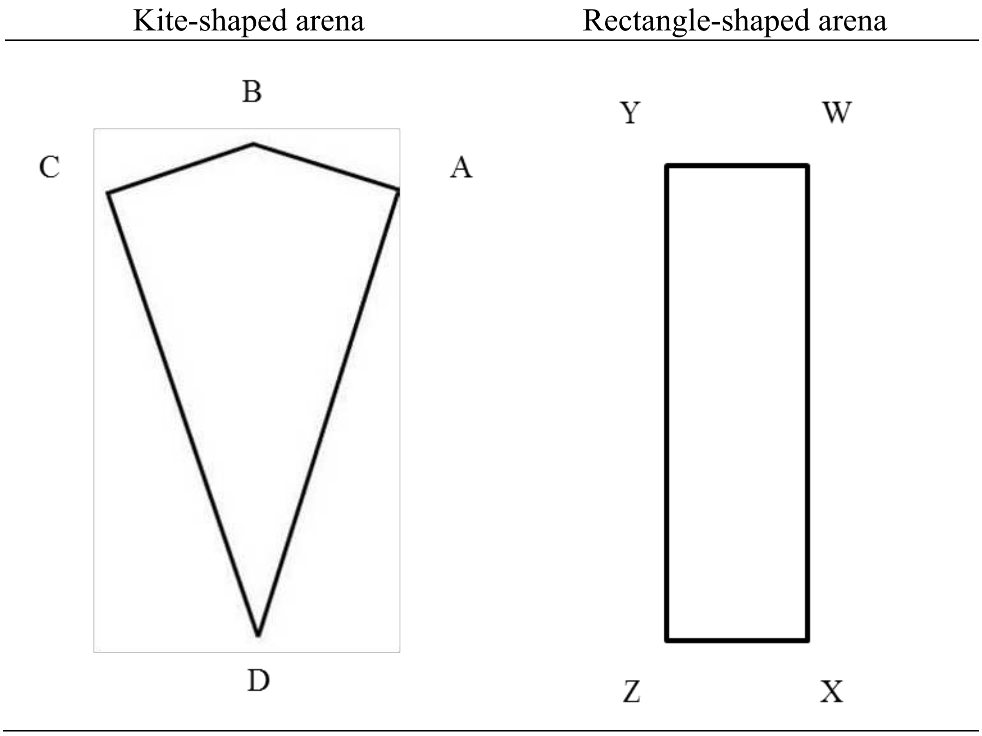


Figure 2.1. Schematic views of the kite- and rectangle-shaped arenas of Experiment 1. Letters are used to denote individual corners of each shape.

Transfer tests. Following 16 acquisition trials, participants immediately received two transfer tests in which the hidden goal was removed, and participants were allowed to search for 60 seconds. For participants who received acquisition trials in a kite-shaped arena, the transfer tests were conducted in rectangle-shaped arenas (group kite-rectangle) and, for participants who received acquisition trials in a rectangle-shaped arena, the transfer tests were conducted in kite-shaped arenas (group rectangle-kite). One transfer test was conducted in an arena which was the same colour as the acquisition arena, whilst the second was conducted in an arena which was a different colour to the acquisition arena (see Figure 2.2). The order of the same and different colour transfer tests was counterbalanced across participants.

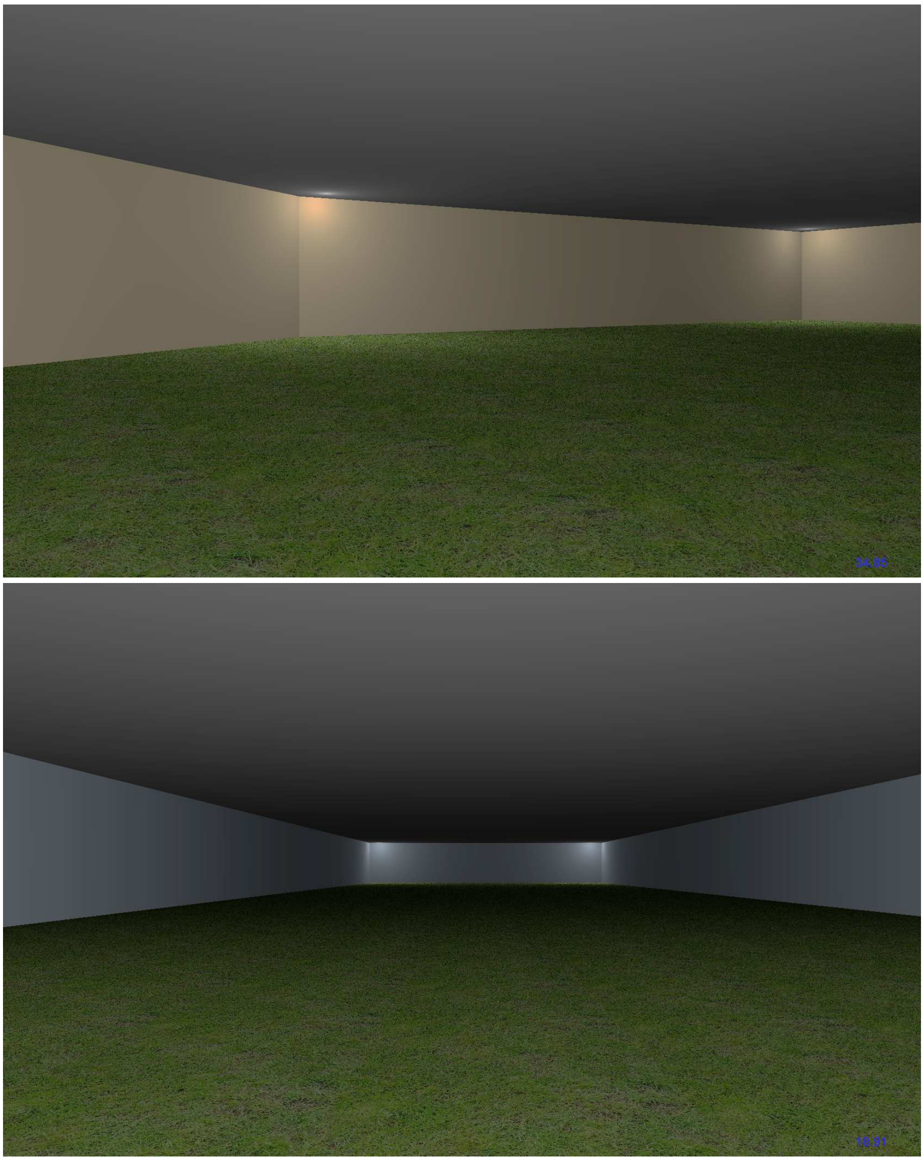


Figure 2.2. Examples of the kite-shaped (top) and rectangle-shaped (bottom) arenas used in Experiment 1.

Navigational performance during the transfer tests was analysed using two methods. First, the time spent in 3.24m x 3.24m square search zones that were placed at corners A and C of the kite-shaped arena (see Figure 2.1) was measured, and at all four corners of the rectangle-shaped arena. Assessing spatial behaviour during extinction tests (where no hidden goal is present) in such a manner is common in experiments conducted with animals (McGregor et al., 2009), and humans (Redhead & Hamilton, 2009). Second, following Pearce et al. (2004), the corner of the arena which participants first visited during the test trials was also recorded. In order to be consistent with the zone analysis described above, a participant was deemed to enter a particular corner once they were within 3.24m from the point where two walls joined.

2.1.2 Results

2.1.2.1 Acquisition

Figure 2.3 shows that the latency, in seconds, from the beginning of each acquisition trial to enter the region defined as the hidden goal decreased during the acquisition trials conducted in both kite- and rectangle-shaped arenas. A two-way analysis of variance (ANOVA) conducted on individual latencies to find the goal, with a between-subjects factor of group (kite-rectangle or rectangle-kite) and a within-subjects factor of trial (1-16), revealed no significant main effect of group, $F<1$, but a significant main effect of trial, $F(15, 450) = 19.04$, $MSE = 478.94$, $p< .001$, $\eta_p^2 = .39$, and a significant interaction between group and trial, $F(15, 450) = 2.46$, $MSE = 478.94$, $p= .002$, $\eta_p^2 = .08$. Participants in both groups became quicker to find the goal as trials progressed, however, participants trained in the kite-shaped arena were marginally slower to find the hidden goal on trial 1 compared to participants trained in the rectangle-shaped arena, $F(1, 30) = 3.28$, $MSE = 4318.34$, $p= .08$, $\eta_p^2 = .10$. There were no other significant differences between groups on remaining trials, $Fs(1, 30) < 1.77$, $MSEs < 1369.39$, $ps > .19$, $\eta_p^2 < .06$.

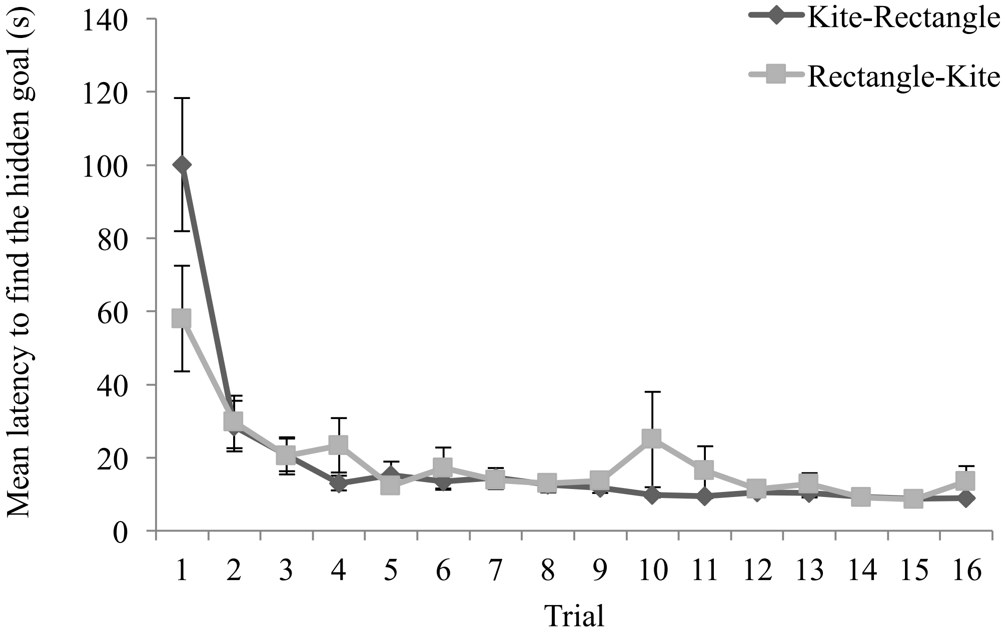


Figure 2.3. Mean latencies, for both the kite-rectangle and rectangle-kite groups, to find the hidden goal during the acquisition trials of Experiment 1. Error bars represent ± one standard error of the mean.

2.1.2.2 Transfer tests

Zone analysis. Figure 2.4 displays the time, in seconds, that participants in both the kite-rectangle and rectangle-kite groups spent searching for the hidden goal, in both the correct and incorrect zones during the transfer tests. Correct zones were defined as the right-angled corners of the test environment that shared the same local geometric cues as the corner that signalled the goal location during acquisition, and incorrect zones were defined as the other right-angled corner(s). For participants in group rectangle-kite, there was a clear preference for searching in the correct zone, over the incorrect zone, during the same colour transfer test. The same preference, albeit attenuated, was also apparent in the different-colour transfer test for this group. Participants in group kite-rectangle also preferentially searched in the correct zone, over the incorrect zone, during the same colour transfer test. In the different-colour transfer test, however, participants in group kite-rectangle did not preferentially search in either of the two zones over the other. A three-way ANOVA conducted on individual time spent in zones, with a between-subjects factor of group (kite-rectangle or rectangle-kite), and within-subjects factors of test colour (same or different) and zone (correct or incorrect), revealed no significant main effect of test colour, $F<1$, but a significant main effect of group, $F(1, 30) = 4.32$, $MSE = 40.83$, $p = .046$, $\eta_p^2 = .13$, in which group kite-rectangle spent significantly more time in the measured zones than group rectangle-kite. There was also a significant main effect of zone, $F(1, 30) = 14.46$, $MSE = 54.56$, $p = .001$, $\eta_p^2 = .33$, as well as a significant interaction between zone and test colour, $F(1, 30) = 4.28$, $MSE = 54.56$, $p = .047$, $\eta_p^2 = .13$. In both the same colour test, $F(1, 30) = 10.88$, $p = .003$, $\eta_p^2 = .27$, and the different colour test, $F(1, 30) = 5.10$, $p = .031$, $\eta_p^2 = .15$, participants searched for significantly longer in the correct zone compared to the incorrect zone. Across test colours, the amount of time participants spent in the correct zone did not significantly differ, $F(1, 30) = 1.89$, $p = .18$, $\eta_p^2 = .06$; however, participants spent significantly longer in the incorrect zone during the different colour test compared to the same colour test, $F(1, 30) = 6.49$, $p = .016$, $\eta_p^2 = .18$. Returning to the results of the overall ANOVA, the remaining interactions between zone and group, $F(1, 30) = 1.90$, $MSE = 54.56$, $p = .18$, $\eta_p^2 = .06$, between group and test colour, $F < 1$, and the three-way interaction between zone, group, and test colour, $F < 1$, were not significant.

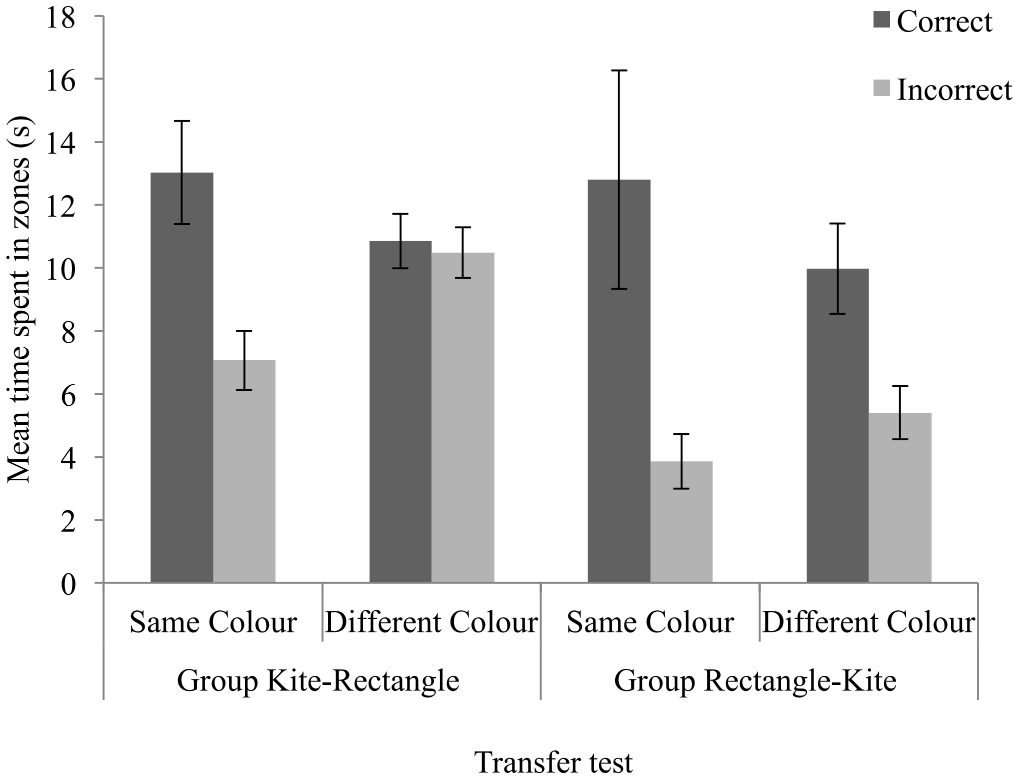


Figure 2.4. Mean time spent in the correct and incorrect zones, for both the kite-rectangle and rectangle-kite groups, during the same and different colour transfer tests of Experiment 1. Error bars represent ± one standard error of the mean.

First-choice analysis. Table 2.1 displays the number of participants in group rectangle-kite that visited the correct, incorrect, acute, or obtuse corner of the same colour, and different colour, kite-shaped test arenas. Table 2.2 shows the number of participants in group kite-rectangle that visited the correct, or incorrect, corners of the same colour, and different colour, rectangle-shaped test arenas. In both groups, for both coloured tests, at least 75% of participants entered the correct corner first during the test trial.

Table 2.1. The number of participants (out of 16) in group rectangle-kite that visited the correct, incorrect, acute, or obtuse corner first during the same, and different, colour transfer tests.

		Transfer test	
		Same colour	Different colour
Zone	Correct	12	12
	Incorrect	1	0
	Acute	1	2
	Obtuse	2	2

Table 2.2. The number of participants (out of 16) in group kite-rectangle that visited the correct, or incorrect, corner first during the same, and different, colour transfer tests.

		Transfer test	
		Same colour	Different colour
Zone	Correct	14	12
	Incorrect	2	4

Pearce et al. (2004) suggested two navigational strategies that would lead participants to the correct corner of a test environment. First, according to a *local* strategy, participants navigate to the corner of the test arena that shared the same local geometric cues as the corner that signalled the goal location during acquisition. Second, according to a *single-wall* strategy, participants learn to navigate to one end of a particular wall during acquisition. For instance, if the goal was present in corners W and Z of the rectangle displayed in Figure 2.1, then participants could have learned to navigate to the left end of a long wall. If this behaviour was transferred to the kite-shaped test environment, participants would be expected to navigate to the left end of wall AD (the correct corner), or the left end of wall CD (the acute corner). Alternatively, participants may have navigated to a particular end of a short wall. If the goal was present in corners W and Z of Figure 2.1, then participants could learn to navigate to the right end of a short wall. If this behaviour was transferred to the kite-shaped test arena, participants would navigate either to the left end of wall AB (the correct corner) or the left end of wall CB (the obtuse corner).

By analysing the first-choice behaviour of group rectangle-kite, it is possible to determine which strategy participants were using in the current experiment by process of elimination. If participants were using a local strategy, it would be expected that there would be significantly more first visits to the correct corner, over any other corner, at test. In contrast, the single-wall strategy predicts that participants will visit the correct corner first on only half of the test trials. For the other half of the test trials, participants would be expected to visit either the acute or obtuse corner, depending on whether they used a long or short wall strategy. By following a single-wall strategy, the probability of choosing the correct corner, over both the acute and obtuse corners combined, is .5. Across both test trials given to group kite-rectangle, the correct corner was visited first on 24 out of 32 occasions. A sign test revealed that this outcome was significantly greater than chance, $p = 0.007$; thus, providing evidence that participants were not using a single-wall strategy. For the sake of completeness, across both tests administered to group kite-rectangle, participants navigated to the correct corner first on 26 out of 32 occasions. A sign test revealed that this outcome was significantly different to chance, $p < 0.001$.

2.1.3 Discussion

Following training in which participants were required to find a goal hidden in one of the right-angled corners of either a kite- or rectangle-shaped environment, participants were transferred to a rectangle- or kite-shaped testing environment, respectively. Within these test environments participants spent more time exploring the corner that had the same geometric cues of the corner that was closest to the goal in the training environment, both when the colour of the environment at test was the same, and when it was different, to the colour of the environment from training. Participants also displayed a significant preference for navigating to the correct corner first during a test trial. Together, these results are consistent with other experiments that have demonstrated similar navigational transfer effects across environments of different shapes (e.g. Lew et al., 2014; McGregor et al., 2006; Pearce et al., 2004; Poulter et al., 2013; Tommasi & Polli, 2004), and are consistent with the idea that, during training, participants used local-shape information in order to find the hidden goal. For example, during training, participants may have learned that approaching an egocentrically-encoded scene, such as the conjunction of two walls of different lengths, was associated with the goal (Cheung, Stürzl, Zeil, & Cheng, 2008; McGregor et al., 2006; Pearce et al., 2004; Stürzl, Cheung, Cheng, & Zeil, 2008). As the same, or a similar, scene is present during the test trials, this navigational behaviour will transfer from training. It is rather more difficult to explain these results in terms of a theory of spatial navigation that proposes a global representation of the overall shape of the environment is learned during training (Cheng, 1986; Gallistel, 1990; Wang & Spelke, 2002, 2003). If this were the case, then the change in the overall shape of the environment between training and testing should have removed any preference for searching in one right-angled corner over another. This was not observed.

It is worthwhile discussing the interaction between group and trial that was observed during acquisition, and the main effect of group that was observed at test. These effects were most likely observed because, compared to the kite-shaped arena, the rectangle-shaped arena had twice as many goals and zones during acquisition and test. During the first acquisition trial, participants will be unaware of the hidden-goal's location. Consequently, participants will be more likely to find the goal by chance in the rectangle-shaped environment that contained two hidden goals, compared to the kite-shaped arena that contained one hidden goal. Similarly, at test, there were two correct and incorrect zones in the rectangle-shaped arena, compared to one of each zone in the kite-shaped arena. It would, therefore, be expected that participants who were tested in a rectangle-shaped environment would spend more time in zones, overall, than participants tested in a kite-shaped environment, as there were more zones in which participants could traverse.

Figure 2.4 shows that, when the colour of the training and test environments differed, the transfer of navigational behaviour from a rectangle to a kite was, at least numerically, less susceptible to generalisation decrement relative to the transfer of navigational behaviour from a kite to a rectangle, although it is worth noting here the lack of a three-way interaction to confirm this finding. Experiments 2 and 3 were designed to assess the extent to which local geometric information could be blocked by, and block, learning about wall-colour information, respectively. In order to achieve this, and as will be seen, it was necessary to transfer participants to different-coloured arenas. In order to protect the effect from generalisation decrement, this transfer was from a rectangle to a kite, and not vice versa.

2.2 Experiment 2

The current experiment was designed to assess if learning about local geometric cues is subject to blocking from prior learning about non-geometric wall colours, in the manner predicted by Miller and Shettleworth (2007, 2008, 2013), who proposed that elements that are present at given locations within an environment can gain and lose associative strength. As noted in the introduction to this chapter, evidence that appears consistent with this prediction was provided by an experiment conducted by Pearce et al. (2006), in which rats were initially trained to locate a hidden platform on the basis of different-coloured walls in a square-shaped arena. In a subsequent stage of training, the rats were placed into a rectangle-shaped arena, and again had to find a submerged platform. For experimental rats, the wall colours that signalled the goal location in stage 1 of the experiment continued to signal the goal location in the stage 2. For control rats, however, the wall colours that signalled the goal location in stage 1 no longer signalled the goal location in the stage 2. In a test trial conducted in extinction, and in which all the walls were the same colour, control rats spent significantly longer searching in the corner of the rectangle where the platform had been located compared to the experimental rats. For rats in the experimental group, the coloured-wall information blocked learning about the geometry of the rectangle-shaped arena. As the test arena was the same shape as the stage 2 arena, however, it is not possible to determine whether Pearce et al. (2006) detected blocking of global-shape learning or, instead, blocking of local geometric learning (see also: Horne & Pearce, 2009a; Wilson & Alexander, 2008).

In order to address the difficulty in interpreting the results of previous blocking studies, the design of Pearce et al. (2006) was adapted so that the test arenas in the current experiment contained the same local-shape cues as the arena used for stage 2 training but, importantly, the global-shape of these two environments were different. Any difference in test trial performance between the experimental and control groups, therefore, would be due to cue competition based upon a representation of local-shape information, and not a representation of the global-shape. In stage 1, participants were trained to find a hidden goal in a square-shaped arena that comprised two adjacent blue walls and two adjacent cream walls. For an experimental group, the goal was located in a corner where, for example, a blue wall was to the right of a cream wall. For a control group, the goal was located in a corner where a blue wall was to the left of a cream wall. In stage 2, participants were transferred to a rectangle-shaped environment that also comprised two adjacent blue walls and two adjacent cream walls. For both groups, the hidden goal was located, for example, in the corner where a long blue wall was to the right of a short cream wall. Consequently, participants in both groups could rely on the shape of the environment to find the hidden goal, or the colour of the walls. For the experimental group only, the colour of the walls that signalled the goal location in stage 1 continued to signal the goal location in stage 2. In contrast, for the control group, the colour of walls that signalled the goal location in stage 1 no longer signalled the goal location in stage 2 (see Figure 2.5).

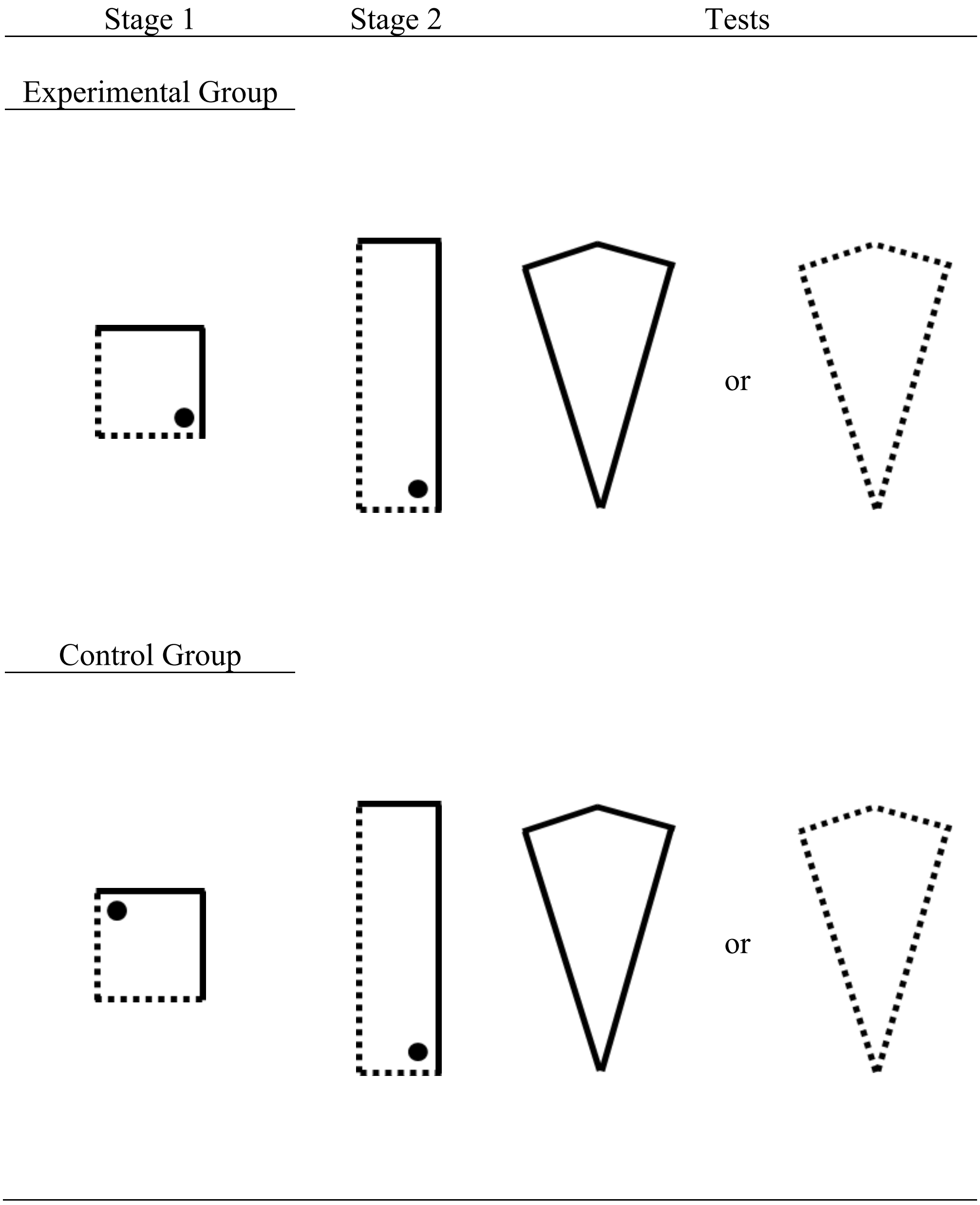


Figure 2.5. An example of the trials given to the experimental and control groups during Experiment 2. The dotted and solid lines represent different coloured walls, and the black filled circles represent the location of the hidden goal. Participants received one test trial in a kite-shaped arena, the colour of which was counterbalanced across participants.

In order to assess if participants had acquired any knowledge of the local-shape information that predicted the goal location in stage 2, participants were given two 60 second test trials in a kite-shaped arena that contained no hidden goals. If learning about local geometric cues proceeds in a manner consistent with the theory proposed by Miller and Shettleworth (2007, 2008, 2013), the associative strength of the coloured walls in the goal location should prevent the experimental group learning the association between the local geometric cues and the goal location in stage 2 of the experiment. This group, therefore, should show no preference for any corner of the kite-shaped arena in the final test trials. For the control group, the associative strength of the coloured walls in the goal location during stage 2 will initially be low because, in stage 1 of the experiment, this wall colour did not signal the goal location. Consequently, the local-shape information may enter into an association with the hidden goal and, thus, participants in the control group would be expected to show a preference for the corner of the kite that shares the same local-shape properties as the corner of the rectangle that signalled the goal location in stage 2.

2.2.1 Method

2.2.1.1 Participants

32 participants were recruited from the University of Nottingham (20 female), and were given course credit in return for participation. The age of participants ranged from 18 to 46 years (mean = 22.81, *SD* = 5.34). Participants were pseudo-randomly assigned to each group in order to ensure an equal number of males and females were allocated to the experimental and

control groups. A £10 prize was awarded to the participant who completed the experiment in the shortest time.

2.2.1.2 Materials

All virtual environments were created and displayed as described in Experiment 1. The cream and blue coloured walls that are referred to in the following procedure section are also the same as described in Experiment 1. In Experiment 2, a square-shaped arena was employed in stage 1. Assuming a walking speed of 2 m/s, the perimeter of the square was 72m, with each wall being 18m in length. The height of the walls creating the square was, again, approximately 2.5 m and, as with the kite- and rectangle-shaped arenas, the goal within the square-shaped arena was a square region (1.08m x 1.08m, invisible to participants), the centre of which was always located 2.48m away from the walls of the arena, along on a notional line that bisected a right-angled corner.

2.2.1.3 Procedure

General. All general details were the same as reported for Experiment 1, save for minor changes to the instructions. Participants were informed that there would be 30 trials in the experiment, and that the session would last around 20 minutes.

Stage 1. Participants were first required to complete 16 trials in a square-shaped arena, which comprised two adjacent cream walls, and two adjacent blue walls (see Figure 2.6). Participants began each trial at the centre of the arena, and the direction in which participants began facing was

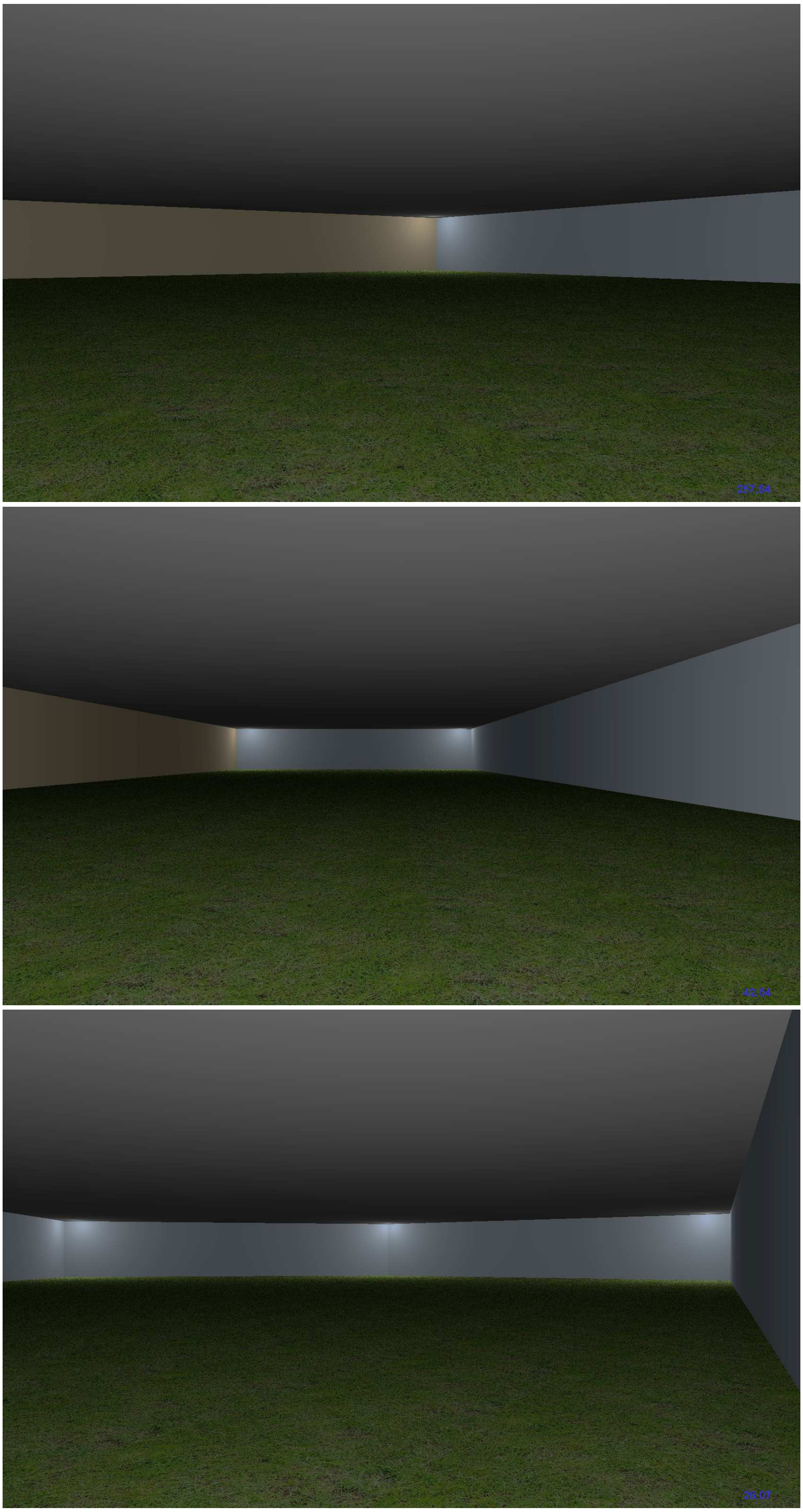


Figure 2.6. Examples of the square-shaped (top), rectangle-shaped (middle), and kite-shaped (bottom) arenas used in Experiment 2.

randomised for every trial. For both experimental and control groups, the hidden goal was located in a corner where two differently-coloured walls met. For half of the participants in each group the hidden goal was located in a corner where a cream wall was to the left of a blue wall. For the remaining participants in each group, the goal was located in the corner where a blue wall was to the left of a cream wall.

Stage 2. Immediately after completing stage 1, participants completed 12 trials in a rectangle-shaped arena. Like the square-shaped arena of stage 1, the rectangle-shaped arena in stage 2 consisted of two adjacent cream walls, and two adjacent blue walls (see Figure 2.6). For the experimental group, the coloured walls that previously predicted the goal location in the square-shaped arena of stage 1 continued to predict the goal location in the rectangle-shaped arena in stage 2. For the control group, however, the coloured walls that previously signalled the goal location in stage 1 no longer signalled the goal location in stage 2. The goal, instead, was located at the corner of the rectangle-shaped arena that was a mirror image of the coloured walls that signalled the goal location in stage 1. For example, if the goal was located in a corner where a cream wall was to the left of a blue wall in stage 1, then the goal would be located in a corner where a blue wall was to the left of a cream wall in stage 2. The colour of the walls forming the rectangle-shaped arena was fully counterbalanced with the positioning of the goal within the arena.

Test trials. Participants received two test trials, each of which, as reported for the previous experiment, contained no hidden goal. For each test, participants were allowed to search for 60 seconds in a kite-shaped arena. The first test trial was administered after participants had completed four trials of stage 2, whilst the second test trial was administered after participants had completed 12 trials of stage 2 training. Each participant received two tests with arenas that were the same colour. For half of the participants this was blue, and for the remaining participants this was cream. As described for Experiment 1, the time spent within search zones were used to measure navigational performance during these test trials.

2.2.2 Results

2.2.2.1 Stage 1

The top panel of Figure 2.7 shows the latency, in seconds, from the beginning of each trial to enter the region defined as the hidden goal for both the experimental and control groups. Both groups displayed a reduction in latencies across the early training trials. A two-way ANOVA conducted on individual latencies to find the goal, with a between-subjects factor of group (experimental or control) and a within-subjects factor of trial (1-16), revealed a significant main effect of trial, $F(15, 450) = 45.29$, $MSE = 288.84$, $p < .001$, $\eta_p^2 = .60$, confirming that participants became quicker to find the goal as training progressed. There was no main effect of group, $F(1, 30) = 3.85$, $MSE = 563.25$, $p = .06$, $\eta_p^2 = .11$; however, the interaction between trial and group was significant, $F(15, 450) = 2.20$, $MSE = 288.84$, $p = .006$, $\eta_p^2 = .07$. Simple main effects analysis revealed that the control group found the goal faster only on trials 4 and 9, $F\text{s}(1, 30) > 4.28$, $p\text{s} < .047$, $\eta_p^2 = .13$.

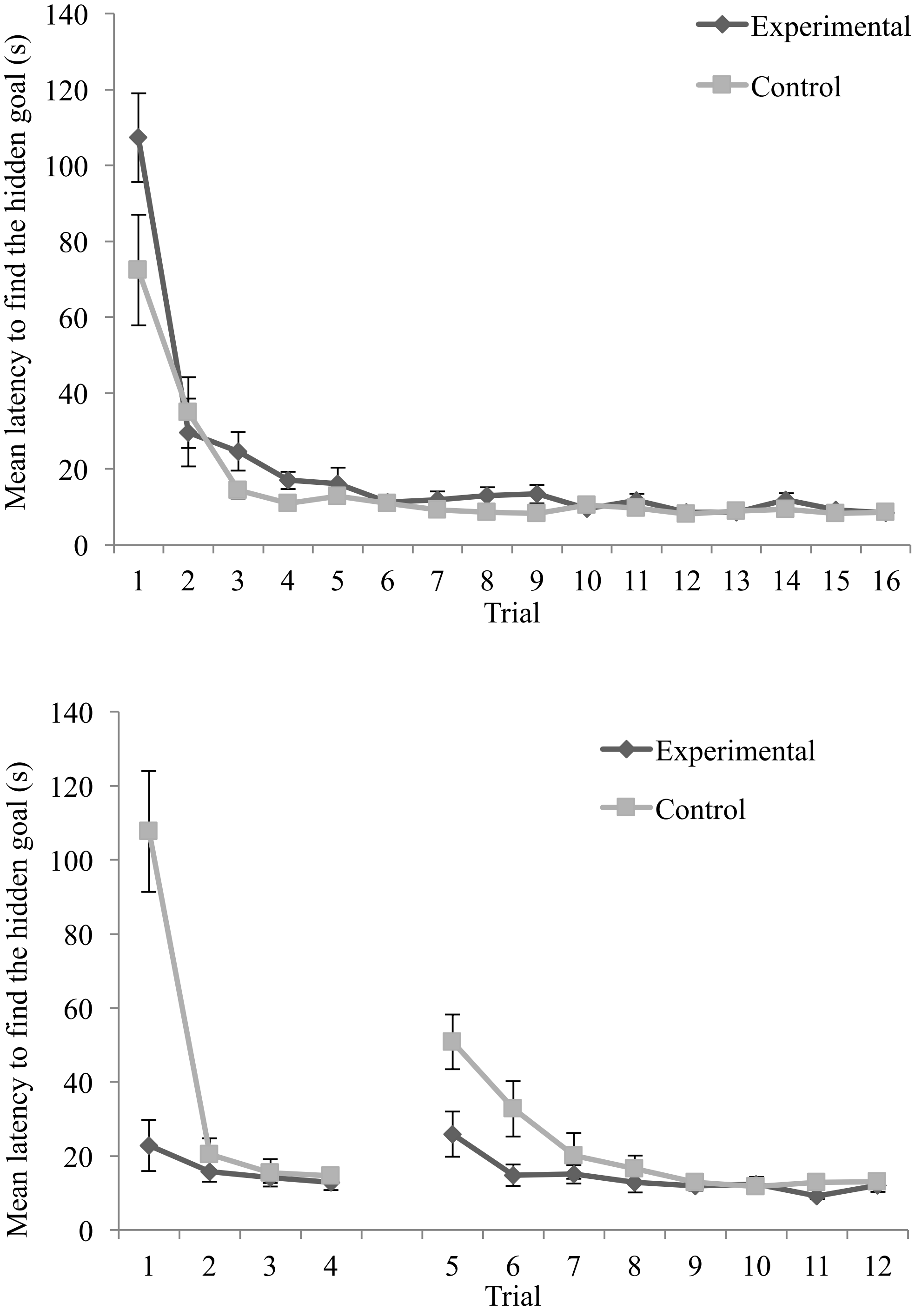


Figure 2.7. Mean latencies, for both the experimental and control groups, to find the hidden goal during stage 1 (top) and stage 2 (bottom) of Experiment 2. Error bars represent ± one standard error of the mean.

2.2.2.2 Stage 2

The bottom panel of Figure 2.7 shows the latency, in seconds, from the beginning of each trial to enter the region defined as the hidden goal for both the experimental and control groups. Mean latencies to find the goal were quicker in the experimental group, compared to the control group, on trials 1, 5, and 6 but there was little indication of any difference between the groups during trials immediately before the two test trials. A two-way ANOVA conducted on individual latencies to find the goal, with a between-subjects factor of group (experimental or control), and a within-subjects factor of trial (1-12), revealed a significant main effect of trial, $F(11, 330) = 24.35$, $MSE = 327.26$, $p < .001$, $\eta_p^2 = .45$, of group, $F(1, 30) = 11.82$, $MSE = 1253.92$, $p = .002$, $\eta_p^2 = .28$, and a significant interaction between trial and group, $F(11, 330) = 14.14$, $MSE = 327.26$, $p < .001$, $\eta_p^2 = .32$. Simple main effects analysis revealed that the experimental group were significantly faster to find the goal on trials 1, 5, and 6, $F\text{s}(1, 30) > 4.92$, $p\text{s} < .034$, $\eta_p^2 > .14$.

2.2.2.3 Test trials

Figure 2.8 shows the amount of time, in seconds, that participants spent in both the correct and incorrect zones averaged across the two test trials. The correct zone was defined as the right-angled corner of the kite-shaped arena that shared the same local geometry as the corner of the rectangle-shaped arena that contained the hidden goal in stage 2. The incorrect zone was defined as the other right-angled corner of the kite-shaped arena. The experimental group spent no more time searching for the goal in the correct

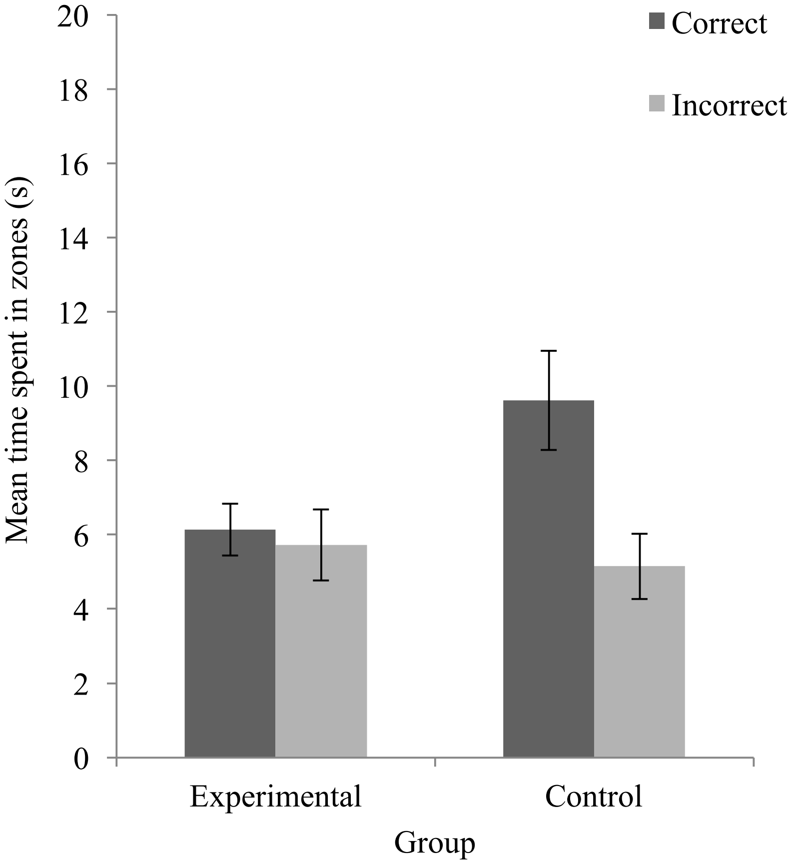


Figure 2.8. Mean time spent, for both the experimental and control groups, in the correct and incorrect zones during the test trial of Experiment 2. Error bars represent ± one standard error of the mean.

zone, over the incorrect zone. In contrast, the control group spent more time in the correct, than the incorrect, zone. A three-way ANOVA conducted on individual times spent in zones, with a between-subjects factor of group (experimental or control), and within-subjects factors of zone (correct or incorrect) and test (first or second), revealed no significant main effect of group, $F(1, 30) = 1.77$, $MSE = 38.35$, $p = .19$, $\eta_p^2 = .06$, or test, $F<1$. There was, however, a significant main effect of zone $F(1, 30) = 7.61$, $MSE = 25.08$, $p=.010$, $\eta_p^2 = .20$, and a significant interaction between zone and group $F(1, 30) = 5.26$, $MSE = 25.08$, $p=.029$ $\eta_p^2 = .15$. Simple main effects analysis of this interaction revealed that the control group spent more time searching in the correct zone than the experimental group, $F(1, 30) = 5.33, p=.028, \eta_p^2 = .15$. There was, however, no difference in the time spent in the incorrect zone between the experimental and control groups, $F<1$. Within groups, the experimental group did not spend more time in the correct zone than the incorrect zone, $F<1$, whereas the control group did spend more time in the correct zone, compared to the incorrect zone, $F(1, 30) = 12.76, p= .001, \eta_p^2 = .30$. The remaining two-way interactions between test and group, test and zone, and the three-way interaction were not significant, *F*s<1.

2.2.3 Discussion

Participants received training in which a hidden goal was located in a distinctively-coloured corner of a rectangle, before receiving test trials in a kite-shaped arena. For an experimental group, the distinctively-coloured corner had previously signalled the hidden goal in a square arena, and this resulted in participants spending no more time in the correct, than the incorrect, zone in the kite-shaped arena during the final test stage. In contrast, for the control group, the distinctively coloured corner had not been previously established as a cue for the hidden goal, and this resulted in the control group spending more time in the correct than the incorrect zone of the kite-shaped arena during the test. These data, therefore, constitute a demonstration of blocking, and concord with those obtained by Pearce et al. (2006), who also demonstrated that establishing a wall colour as a cue for a goal location could block subsequent learning about the location of a hidden goal with respect to the shape of the arena. For the current experiment, however, the shape of the arena was changed between stage 2 and testing, thus, the learned information that permits navigation to transfer between arenas of different shapes is susceptible to blocking. On the basis of the first-choice data analysed in Experiment 1, this information is locally encoded (see also Pearce et al., 2004). The current experiment, therefore, suggests that learning about local geometric cues is consistent with the predictions provided by the Miller-Shettleworth model, which suggests that navigation that is based upon the shape of an environment is a consequence of an associative process (Rescorla & Wagner, 1972) that permits cue competition between geometric and non-geometric elements.

The model of navigation proposed by Miller and Shettleworth (2007, 2008, 2013) suggests that learning to navigate on the basis of non-geometric information (e.g. coloured walls) is governed by the same principles as learning to navigate on the basis of the boundary shape of an environment (cf. Cheng, 1986; Gallistel, 1990). Consequently, wall colour should not only be able to block learning about the local-shape information as demonstrated in the current experiment, but vice versa. Experiment 3 was conducted to test the assumption that local-shape information should also be able to block subsequent learning about wall colour.

2.3 Experiment 3

The current experiment was designed to assess if learning about local-shape information would block subsequent learning about wall colour information. In order to do this, the design of Experiment 2 was altered so that participants were placed into a uniformly-coloured rectangle-shaped arena, and required to find a hidden goal in, for example, the corner where a long wall was to the left of a short wall. In stage 2, participants were transferred to a kite-shaped arena, in which the two long walls were a different colour to the two short walls. For the experimental group, the hidden goal was located in a right-angled corner where a long wall was to the left of a short wall. As this corner shares the same local-shape features as the corner that contained the hidden goal in stage 1, the theory proposed by Miller and Shettleworth (2007, 2008, 2013) predicts that participants would not acquire any knowledge about the coloured walls which also predicted the goal location in stage 2. For a control group, the goal was located in the right-angled corner of the kite-shaped arena where a long wall was to the right of a short wall in stage 2. As the local-shape cues at this corner were not paired with the hidden goal in stage 1 for the control group, participants should associate the wall colour with the goal location in this stage. In a final test, participants were given a trial in a square-shaped arena constructed from the same wall colours present in the kite-shaped arena. Participants in the control group, but not the experimental group, were expected to preferentially search in the corner of the square that shared the same colour configuration as the location that contained the hidden goal in the kite-shaped arena from stage 2. The experimental group should show no preference for any corner of the square test-arena.

In the experimental group, the same local geometric cues signal the goal location in both stage 1 and 2 of the experiment. In contrast, for the control group, the local geometric cues that signalled the goal location in stage 2 had previously signalled the absence of the goal location in stage 1. It might, therefore, be expected that the control group would learn less about the local geometric-cues that signal the goal location during stage 2, compared to the experimental group. In order to assess this possibility, learning about the geometric properties of the stage 2 arena in the control group was compared to that of the experimental group by including a test trial in a kite-shaped arena that was built from grey walls. Furthermore, as there was no effect of test in Experiment 2, in the current experiment only one set of tests was administered following 4 trials of stage 2 training.

2.3.1 Method

2.3.1.1 Participants

48 participants were recruited from the University of Nottingham (36 female), and were given course credit in return for participation. The age of participants ranged from 18 to 41 years (mean = 19.92, *SD* = 3.93). Participants were pseudo-randomly assigned to each group in order to ensure an equal number of males and females were allocated to each group. A £10 prize was awarded to the participant who completed the experiment in the shortest time.

2.3.1.2 Materials

The dimensions of the kite- and rectangle-shaped arenas were the same as reported for Experiment 2. The square arena had a perimeter of 54m, with each wall being 13.5m in length. A number of non-spatial (e.g. Denton & Kruschke, 2006; Hall, Mackintosh, Goodall, & Dal Martello, 1977) and spatial (Couvillon, Campos, Bass, & Bitterman, 2001) learning experiments have observed an attenuation, or a complete absence, of blocking when the to-be-blocked cue is of a higher salience than the blocking cue. In order to protect the present experiment from this effect, the salience of the wall colours was reduced, relative to Experiment 2, by making the two different wall colours subtly different shades of pink (RGB: 178, 76, 204) and purple (RGB: 153, 0, 204).

2.3.1.3 Procedure

General. All general details were the same as reported for Experiment 1, save for minor changes to the instructions. Participants were informed that there would be 22 trials in the experiment.

Stage 1. Participants were required to complete 16 trials in a rectangle-shaped arena, the walls of which were either all pink, or all purple, in colour (see Figure 2.9). For half the participants, the hidden goal was located in a corner where a short wall was the left of a long wall whereas, for the other half of the participants, the goal was located in a corner where a long wall was to the left of a short wall. As with Experiment 1, to ensure visits to the correct corner of the rectangle were always rewarded, each rectangle-shaped arena contained two hidden goals. Each goal location was used equally often in each differently coloured arena, and each group was trained to find the goal in each corner an equal number of times.

Stage 2. Following stage 1 training, participants immediately completed 4 trials in a kite-shaped arena which consisted of two pink and two purple walls (see Figure 2.9). In the experimental group, the hidden goal was located in the corner of the kite that shared the same local geometric cues that

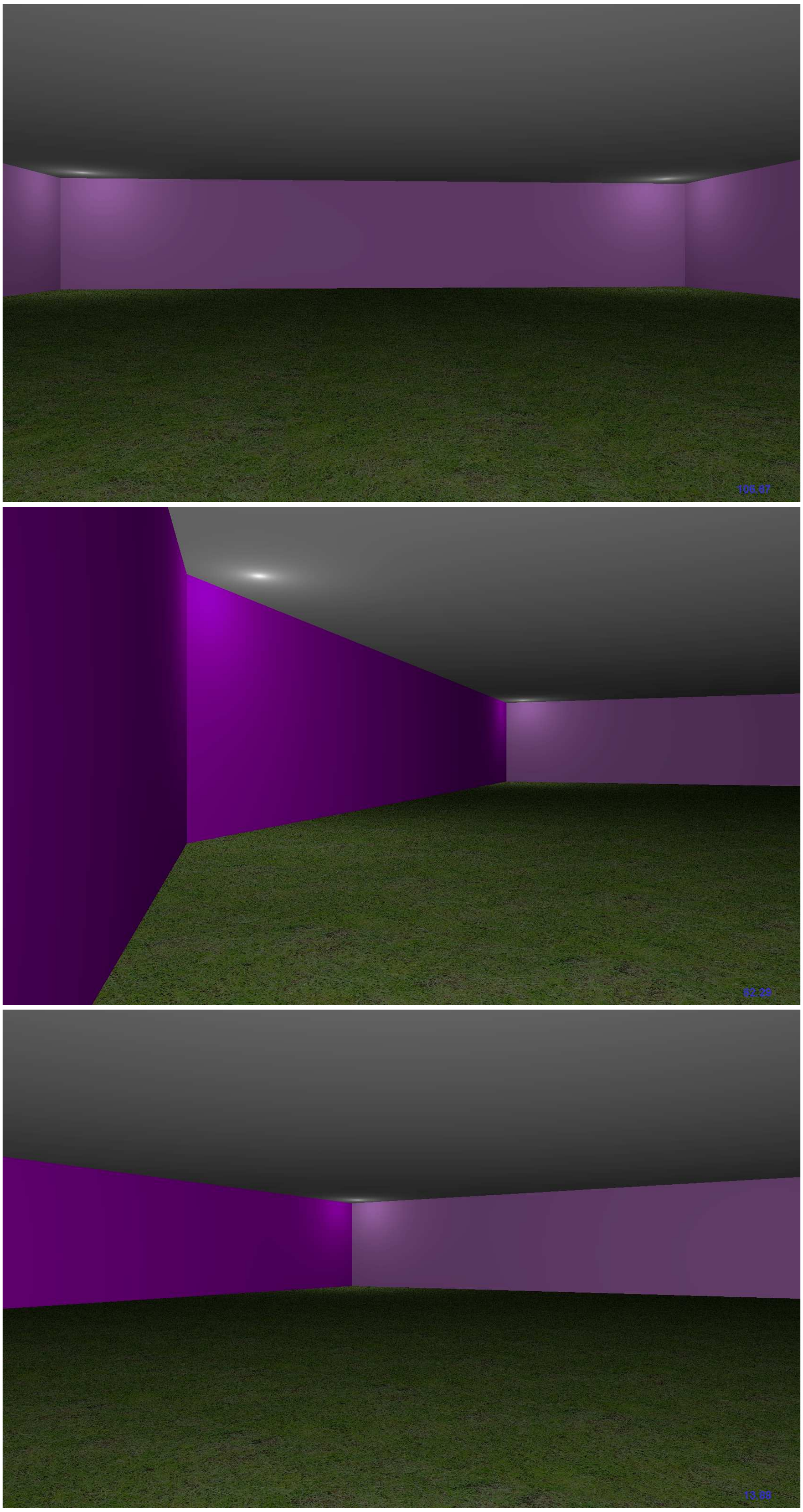


Figure 2.9. Examples of the rectangle-shaped (top), kite-shaped (middle), and square-shaped arenas used in Experiment 3.

signalled the goal location in stage 1. Consequently, if the hidden goal was located in a corner where the short wall was the left of a long wall in the rectangle-shaped arena during stage 1 training, then the goal would be located in the corner where the short wall was the left of a long wall in the kite-shaped arena during stage 2 (see Figure 2.10). For half the participants in the experimental group, the long walls of the kite were purple and the short walls were pink whereas, for the other half of participants, the long walls were pink and the short walls were purple. For the control group, the colour of the walls was counterbalanced in the same manner. In the control group, however, the hidden goal was located in the corner of the kite that shared the same local geometric cues that signalled the absence of the goal in stage 1. For example, following training in which the hidden goal was located in a corner where the long wall was to the left of a short wall in the rectangle-shaped arena during stage 1 training, the goal would be located in the corner where the short wall was to the left of a long wall in the kite-shaped arena during stage 2 (see Figure 2.10 also).

Test trials. After completing stage 2 training, participants were given two test trials, conducted in extinction, both of which lasted for 60 seconds. In the shape test, participants were placed into a kite-shaped arena which consisted of 4 grey walls. In the colour test, participants were placed into a square arena that consisted of two adjacent pink walls, and two adjacent purple walls (see Figure 2.9). The order in which these two tests were administered was counterbalanced across participants. Navigational behaviour in the kite-shaped arena was measured as described for the previous experiments reported here. Behaviour in the square-shaped arena was measured in a similar manner;

however, as the square arena was smaller than the kite-shaped arena, the area of the zones was reduced accordingly. The time spent in square-shaped zones (2.16 x 2.16m), located at the each corner of the square arena, was measured. The centre of these zones was located 2.48m from the corners of the arena, along a line that bisects the corner.

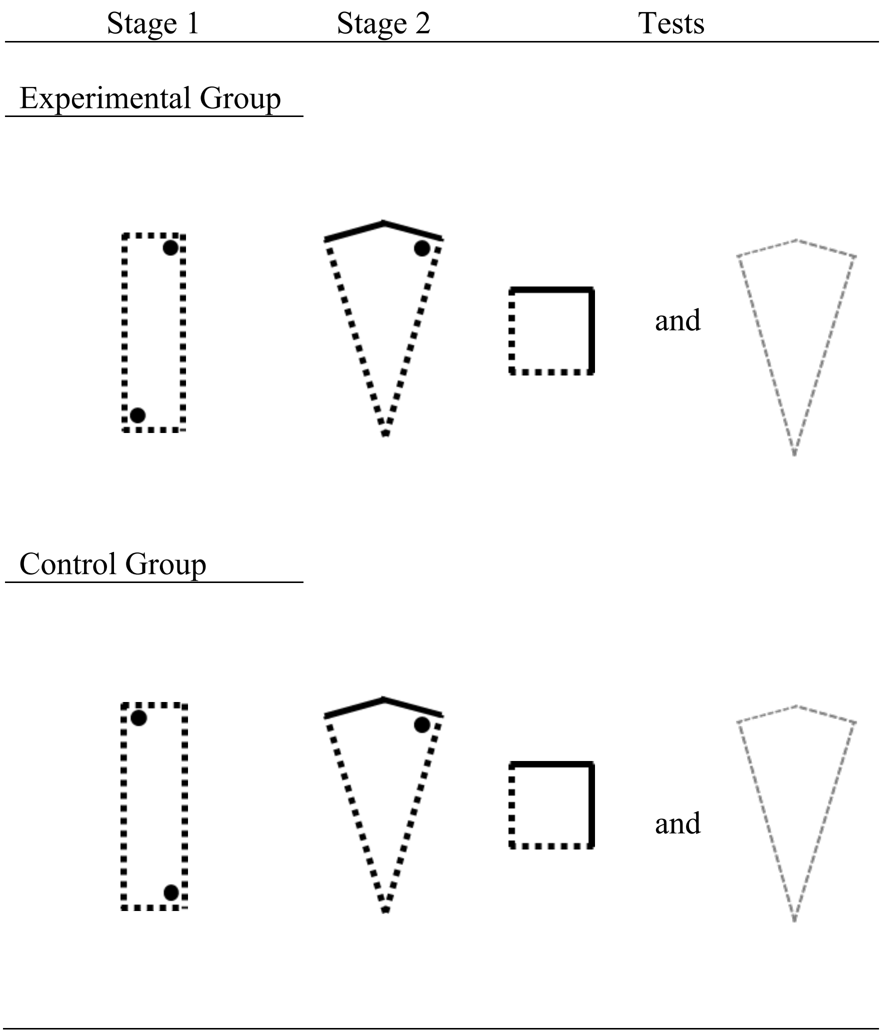


Figure 2.10. An example of the trials given to the experimental and control groups during Experiment 3. The dotted, pecked, and solid lines represent different coloured walls, and the black filled circles represent the location of the hidden goal. Participants received two test trials, one in a square-shaped environment and one in a kite-shaped arena.

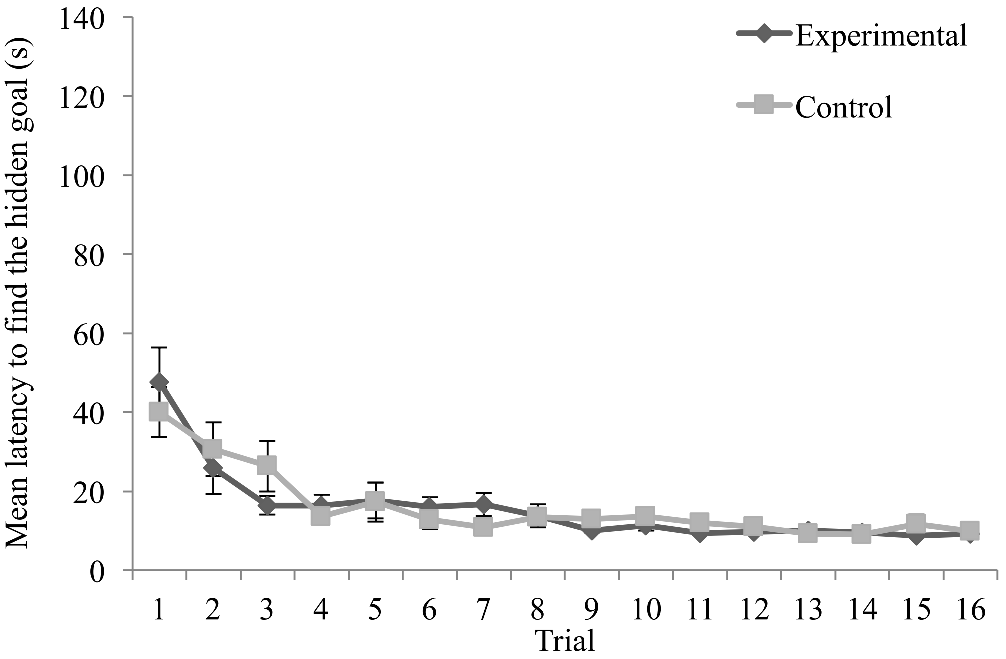
2.3.2 Results

2.3.2.1 Stage 1

The top panel of Figure 2.11 shows the latency, in seconds, from the beginning of each trial to enter the region defined as the hidden goal, for both the experimental and control groups. Mean latencies decreased across the early trials of stage 1, but there was little evidence of any between-groups differences in the latter stages of stage 1. A two-way ANOVA of individual latencies to find the goal, with a between-subjects factor of group (experimental or control), and a within-subjects factor of trial (1-16), revealed a significant main effect of trial, $F(15, 690) = 16.12$, $MSE = 242.26$, $p < .001$, $\eta_p^2 = .26$, confirming that participants took less time to find the hidden goal as stage 1 training progressed. There was, however, no significant main effect of group, and no significant interaction between group and trial, both Fs<1.

2.3.2.2 Stage 2

The bottom panel of Figure 2.11 shows the latency, in seconds, from the beginning of each trial to enter the region defined as the hidden goal, for both experimental and control groups during stage 2. Mean latencies for the experimental group were quicker than the control group on trials 1 and 2, although the performance of the two groups appeared more closely matched on trials 3 and 4. A two-way ANOVA of individual latencies to find the goal, with a between-subjects factor of group (experimental or control) and a within-subjects factor of trial (1-4), revealed significant main effects of trial, $F(3, 138) = 15.67$, $MSE = 681.63$, $p < .001$, $\eta_p^2 = .25$, group $F(1, 46) = 14.44$,



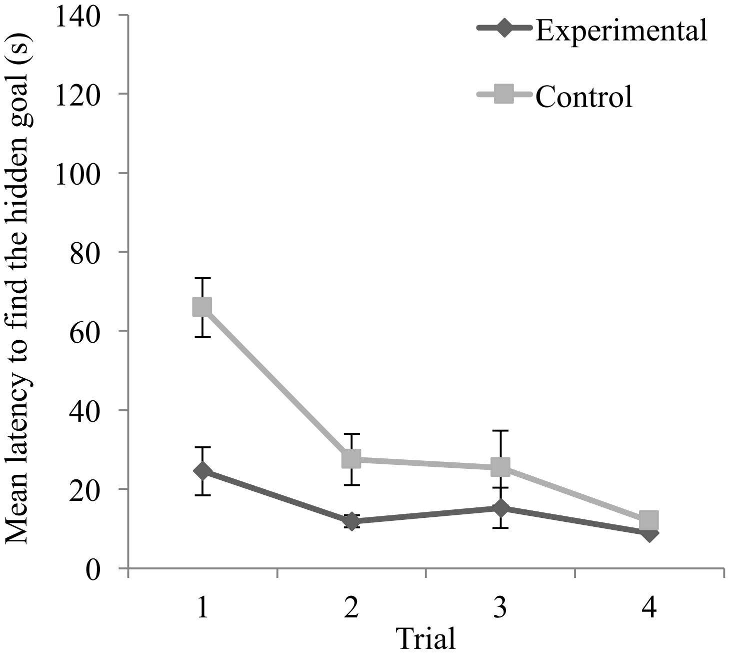
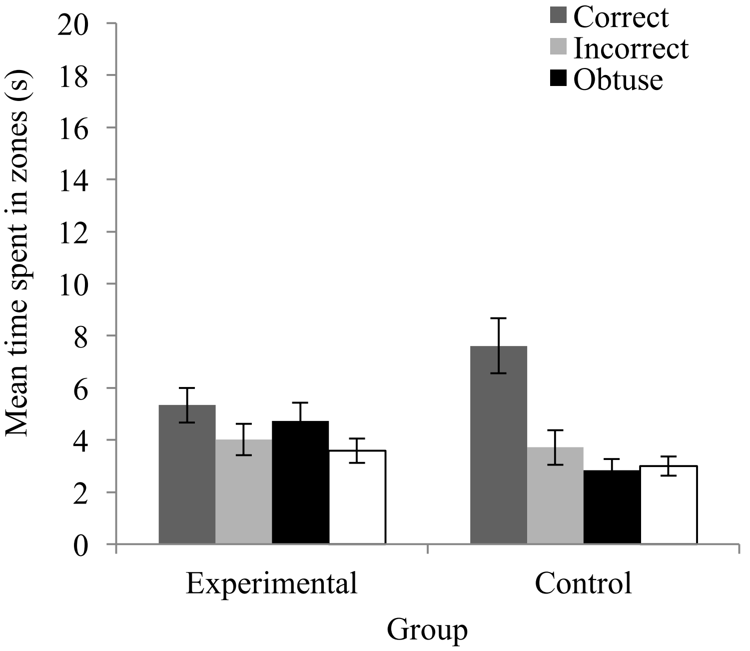


Figure 2.11. Mean latencies, for both the experimental and control groups, to find the hidden goal during stage 1 (top) and stage 2 (bottom) of Experiment 3. Error bars represent ± one standard error of the mean.

MSE = 1021.91, $p < .001$, $\eta_p^2 = .24$, and a significant interaction between group and trial, $F(3, 138) = 4.94$, *MSE* = 681.63, $p = .003$, $\eta_p^2 = .10$. Simple main effects analysis revealed that the experimental group found the hidden goal quicker than the control group on trials 1, 2, and 4, Fs(1, 46) < 18.43, *MSE*s < 1117.64, ps < .024, $\eta_p^2 > .11$.

2.3.2.3 Test trials

Colour test. The top panel of Figure 2.12 shows the amount of time, in seconds, participants spent searching for the hidden goal in all four zones of the square-shaped arena. The wall colours at each corner of the square were the same as those that were present in the kite-shaped arena in which participants navigated during stage 2. Consequently, each corner of the square was identified with reference to the corners that this colour occupied in stage 2. Participants in the experimental group spent an equivalent amount of time in each of the four search zones. In contrast, participants in the control group showed a preference for searching in the correct zone of the arena, relative to the remaining three zones. A two-way ANOVA, conducted on individual time spent in zones, with a between-subjects factor of group (experimental or control), and a within-subjects factors of zone (correct, incorrect, obtuse, or acute), revealed no significant main effect of group, $F < 1$. There was, however, a significant main effect of zone, $F(3, 138) = 9.18$, *MSE* = 10.76, $p < .001$, $\eta_p^2 = .17$, and a significant interaction between zone and group, $F(3, 138) = 3.40$, *MSE* = 10.76, $p = .02$, $\eta_p^2 = .07$. Simple main effects analysis showed that participants in the control group preferentially searched in the correct zone over all other zones, *F*(3, 44) = 7.21, $p < .001$, $\eta_p^2 = .33$. In contrast, participants in the experimental group did not spend significantly longer in either of four zones, *F*(3, 44) = 1.39, $p = .26$, $\eta_p^2 = .09$.



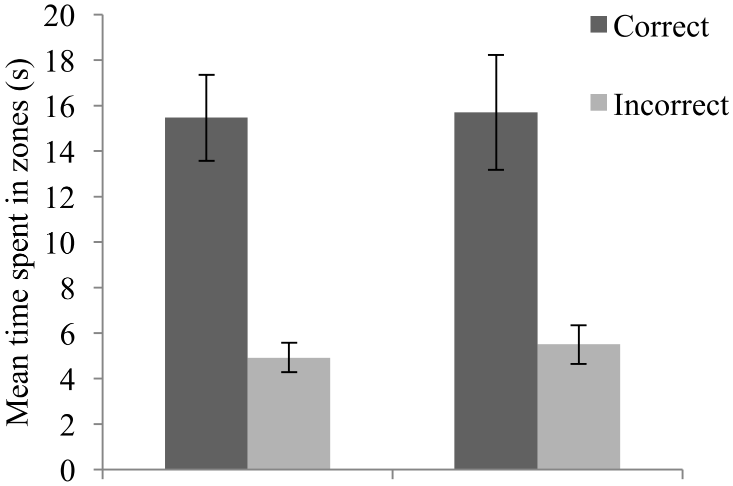


Figure 2.12. Mean time spent, for both the experimental and control groups, in the correct and incorrect zones during the colour test (top panel) and shape test (bottom panel) of Experiment 3. Error bars represent ± one standard error of the mean.

Shape test. The bottom panel of Figure 2.12 shows the amount of time, in seconds, participants spent searching for the hidden goal in both the correct and incorrect zones of the kite-shaped arena. The correct zone was located at the right-angled corner that signalled the goal location during stage 2 training, and the incorrect zone was located at the other right-angled corner. Both the experimental and control groups spent more time searching in the correct zone than the incorrect zone. A two-way ANOVA conducted on individual time spent in zones, with a between-subjects factor of group (experimental or control), and within-subjects factor of zone (correct or incorrect), revealed only a significant main effect of zone, $F(1, 46) = 35.13$, $MSE = 73.46$, $p < .001$, $\eta_p^2 = .43$, confirming that participants spent more time in the correct zone relative to the incorrect zone. There was no significant main effect of group, or a significant interaction between group and zone, both Fs<1.

2.3.3 Discussion

Participants received training in stage 1 in which a hidden goal was located in one of the right-angled corners of a rectangle-shaped arena (e.g. the corner where the long wall is to the left of a short wall). Following this training, participants were required to find the hidden goal in a kite-shaped arena, the walls of which were distinctive colours. For the experimental group, the hidden goal remained in the same right-angled corner as during training (e.g. where the long wall is to the left of the short wall). For the control group, the hidden goal was placed in the other right-angled corner (e.g. where the short wall was to the left of a long wall). Following this training, test trials were administered in a square arena that comprised walls of the same colour as the arena from stage 2. The results of this test revealed that participants in the control group spent longer searching in the corner whose colour was the same as that rewarded during stage 2. The experimental group showed no such preference. This result complements the results of Experiment 2, demonstrating that the geometric cues that permit navigation to transfer between arenas of different shapes are able to prevent (block) learning about the wall colour of the arena.

Interestingly, participants in both groups displayed an equal, and strong, preference for searching in the correct, over the incorrect, corner during a test in which they were placed into a uniformly coloured kite-shaped arena. The experimental group had been consistently rewarded for navigating to the same corner throughout stages 1 and 2; thus, a strong preference for the correct corner was expected in this group. In the control group, however, participants were first trained to navigate to a corner where, for example, a short wall was to the left of a long wall in stage 1, and then trained to navigate to a corner where a long wall was to the left of a short wall in stage 2. Given this inconsistent training, a strong preference for the correct corner in the control group was somewhat surprising. The Miller-Shettleworth model, however, can accommodate this finding because it incorporates a choice rule into the Rescorla-Wagner learning algorithm. If the correct geometry had lower absolute associative strength in the control group, relative to the experimental group, the model can still predict equal performance from both groups so long as the correct corner had higher associative strength than any other corner. For the associative strength of the correct corner in stage 2 to have more associative strength than the incorrect corner in the control group, it is necessary for stage 2 training to reverse the strength of the associative links formed in stage 1. This would be possible if (a) due to generalisation decrement (e.g. Blough, 1975), the associative strength gained by cues in stage 1 did not transfer completely to stage 2, and/or (b) the local geometric cues were more salient than the wall colour information, something that is entirely plausible given that the experiment was conducted with low salience wall colours.

A second possible explanation for the results from the test in the kite-shaped arena is that search behaviour reflects not only the associative strength of the geometric cues of the arena at test, but also the associative strength of the cue that was paired with them during stage 2. It was observed that participants spent more time searching near the correct wall colour in the control than the experimental group and, on this basis, within compound associations from the corner's geometry to the corner's colour might explain these results (see Austen, Kosaki, & McGregor, 2013; Horne & Pearce, 2009b; Rhodes, Creighton, Killcross, Good, & Honey, 2009 for evidence of between cue associations in the spatial domain). Of course, if a similar analysis is applied, vice versa, to the test of the wall colours, then a similar absence of a difference between the experimental and control groups might be expected. To reconcile this, it would be necessary to assume that the within compound association from a corner's geometric cues to its colour is stronger than the within-compound association from the wall colour to the corner's geometric cues.

2.4 General Discussion

In Experiment 1, participants who were trained in a virtual arena to locate a hidden goal in one corner of, for example, a rectangle-shaped arena subsequently expressed a bias towards searching in a corner of the same local geometry that was in an arena of a different global-shape. These results are consistent with comparable experiments conducted with rats (e.g. McGregor et al., 2006; Pearce et al., 2004; Poulter et al., 2013), chicks (e.g. Tommasi & Polli, 2004), and studies of navigation in adults in virtual environments (e.g. Lew et al., 2014). This general effect, in which spatial navigation that is based upon an environment's geometry survives a transformation of its overall shape, has been interpreted as evidence of an encoding of the local geometric cues of an environment during navigation (Pearce et al., 2004; McGregor et al., 2006; Tommasi & Polli, 2004), and the first-choice data from Experiment 1 support this conclusion. This interpretation contrasts with alternative conceptions of spatial navigation based upon the overall shape of the environment, which have proposed a system of encoding that emphasises a more global representation of the environment (e.g. Cheng, 1986; Cheng & Gallistel, 2005; Gallistel, 1990). In Experiment 2, learning the location of a hidden goal with respect to landmark information in a square arena blocked subsequent learning about the goal's location with respect to the local geometric information of a rectangle-shaped arena. Experiment 3 demonstrated that this blocking effect was reciprocal: learning to locate the hidden goal with respect to the geometric cues of a rectangle-shaped environment blocked subsequent learning about landmark information in a kite shaped arena. Together, the results of Experiments 2 and 3 suggest that local geometric cues are permitted to compete with non-geometric cues, for associative strength to a goal location, according to the rules proposed by Miller and Shettleworth (2007, 2008, 2013).

The results of Experiment 2 are consistent with previously reported experiments where landmarks have been observed to block learning about geometric cues (e.g. Pearce et al., 2006). In these experiments, however, test trials were conducted in an arena that was of the same global-shape as the arena used in stage 2 training. Consequently, it is not possible to distinguish whether learning about landmark cues had blocked learning about a representation of global- or local-shape information. Similarly, the results of Experiment 3 are consistent with previous reports of navigation based upon shape information blocking learning about navigation based upon landmarks (e.g. Wilson & Alexander, 2008). Again, however, as an arena of the same overall shape was employed in stages 1 and 2 of these experiments, it is not possible to ascertain whether learning about global- or local-shape cues blocked subsequent learning about landmark cues. Where the current experiments distinguish themselves, then, is through the change of shape between stage 2 and test (Experiment 2), or between stage 1 and stage 2 (Experiment 3). This manipulation isolated learning to local-shape cues alone, and demonstrated that this learning can be blocked by, and block, learning about landmark information in a manner that is consistent with associative models of spatial navigation (e.g. Miller & Shettleworth, 2007, 2008, 2013). The results of Experiments 2 and 3 were not, however, consistent with models of navigation that assume that geometric and non-geometric information do not compete with each other for control of spatial behaviour (e.g. Cheng, 1986; Gallistel, 1990). The results of Experiment 2, moreover, are not consistent with models of navigation that assume learning about landmark cues should not interfere with learning about the boundary shape of an environment (e.g. Doeller & Burgess, 2008).

Cheng and Gallistel (2005) have provided an alternative explanation for demonstrations of transfer of spatial navigation across different-shaped environments. Instead of adopting a local perspective of spatial navigation, Cheng and Gallistel argued that organisms extract the principal axis of the shape in which they are navigating, and search for a goal that is to one side of one end of this axis. As Cheng and Gallistel (2005) demonstrated, an organism could learn to navigate to a particular corner of a rectangle-shaped environment by relying on either the principal axis of the rectangle, or local geometric cues present at the corner. Importantly, when transferred to a kite-shaped arena, navigation that is based on the principal axis or local geometric cues will result in a preference for searching in the corner of a kite-shaped arena that is geometrically congruent to the trained corner of the rectangle-shaped arena. Consequently, it is possible to explain the data observed in Experiment 1 by assuming participants navigated on the basis of the principal axis of the arena (but see: McGregor et al., 2006). Cheng and Gallistel (2005) did not comment on whether, or not, learning about the principal axis is subject to cue competition effects; however, the principal axis is a global-shape parameter, and both of these authors have elsewhere argued global-shape information is immune to interference from non-shape cues (e.g. Cheng, 1986, Gallistel, 1990). To account for the results of Experiments 2 and 3, it is necessary to assume that learning about the principal axis is susceptible to interference from non-geometric cues or, alternatively, concede that the current results are the consequence of navigation based on local geometric cues (e.g. Pearce et al., 2004).

It is possible that the results of Experiments 2 and 3 are amenable to explanations other than blocking. For instance, it might be argued that blocking was not observed in either of these experiments but, instead, a super-conditioning effect was observed in the control groups of each experiment. Here, learning an association between a conditioned stimulus and an unconditioned stimulus is facilitated by presenting the conditioned stimulus in the presence of a cue that has previously been established a conditioned inhibitor (e.g. Rescorla, 1971; Williams & McDevitt, 2002), an effect that has recently been observed in the spatial domain (Horne & Pearce, 2010). Taking Experiment 2 as example, stage 1 training in a square environment would have served to not only establish an excitatory link between the goal location and the coloured walls that predicted its location, but also to establish an inhibitory link between the goal and coloured walls that signalled its absence. Crucially, for the control group only, in stage 2 training that was conducted in a rectangle-shaped arena, the goal was located next to the wall colours that had previously signalled the goal's absence. Consequently, the geometric cues of the rectangle that signalled the goal location in stage 2 were presented with wall colours that were previously established as a conditioned inhibitor in stage 1. This might be expected to promote quicker learning of the geometry-goal location association in the control group, relative to the experimental group. At test, therefore, the control group spent more time searching in the correct corner of the test arena compared to the experimental group.

It is important to note that, at least in terms of associative strength, the Miller-Shettleworth model anticipates a super-conditioning effect in much the same manner as the Rescorla-Wagner model on which it is based. In circumstances where the geometry of a corner and a landmark signal a goal location, therefore, the correct geometric cues are expected to gain more associative strength if the landmark has previously signalled the absence of the goal, relative to if the landmark had not been established as a conditioned inhibitor (see Horne & Pearce, 2010). Importantly, both the Rescorla-Wagner and Miller-Shettleworth models explain this super-conditioning effect, as well as blocking effects, through a summed error term. Both models, therefore, require landmark and geometric information to interact with each other during learning in a manner that is not consistent with the notion that shape information is processed entirely independently to non-shape information (e.g. Cheng, 1986). Indeed, it is very difficult to explain the results of Experiment 2 and 3 without assuming that geometric and non-geometric cues interact during learning.

2.4.1 Conclusion

Spatial learning based upon the shape of the environment transferred to an environment that was a different global-shape, but which shared local geometric information. Learning about this local geometric information was blocked by, and could block, learning about landmark cues. These results are difficult to reconcile with an analysis of spatial navigation that emphasises the role of a global representation of environmental shape that is impervious to cue competition (e.g. Cheng, 1986; Cheng & Gallistel, 2005; Gallistel, 1990).

In contrast, the current results are consistent with the notion that animals encode local geometric information and, importantly, demonstrate that this information competes with non-geometric information for associative strength in a manner consistent with an associative explanation of spatial navigation (Miller & Shettleworth, 2007, 2008, 2013; Pearce, 2009).

Chapter 3

Landmarks interfere with navigation by, and recognition of, global-shape

In Chapter 1, it was noted that the model of learning proposed by Miller and Shettleworth (2007, 2008, 2013), and the Rescorla-Wagner model on which it is based, assume the salience of elements (α) to be fixed. This is an important theoretical shortcoming of the Rescorla-Wagner model, as a number of non-spatial learning experiments have reported effects that are best explained by models that acknowledge that the salience of elements, or the attention paid to them, can vary with learning (e.g. Mackintosh, 1975; see also Esber & Haselgrove. 2011; Le Pelley, 2004; Pearce & Hall, 1980). For instance, Holland (1984) paired a stimulus (X) with either a low value outcome (1 food pellet), or a high value outcome (1 food pellet, followed by 2 more food pellets). Following this training, a second stimulus (Y) was presented in compound with X. Learning about Y was blocked when the same value outcomes were used in both stages of the experiment. In contrast, learning about Y occurred if the value of the outcome was shifted up or down during stage 2 of the experiment (See also: Dickinson, Hall, & Mackintosh, 1976; Haselgrove, Tam, & Jones, 2013). This effect is difficult to explain in terms of the associative strength of each cue (e.g. Rescorla & Wagner, 1972). In the down shift unblocking condition, for example, the omission of the second pair of food pellets should result in Y being established as a conditioned inhibitor. These down- and up-shift unblocking effects are, however, consistent with attentional models of learning, such as that proposed by Mackintosh (1975). According to this model, animals will pay high levels of attention to cue X as a result of stage 1 training. As cue X is a better predictor of the outcome than cue Y in stage 2, and providing the value of the outcome does not change, then attention will fall to cue Y. Consequently, there will be little conditioning to cue Y. Should there be a surprising omission or addition of an outcome in stage 2, however, then Y will no longer be a poorer predictor of the trial outcome than X. This will result in a reinstatement of attention, thus, allowing conditioning to cue Y.

On a similar note, the assumption that the salience of elements is fixed also appears to be an important theoretical shortcoming of the Miller-Shettleworth model, as effects that are consistent with attentional models of learning have also been reported in the spatial domain. For instance, in an experiment conducted by Redhead, Prados, and Pearce (2001), rats were placed into a circular pool of water, and were initially required to swim to a platform that had a beacon attached to it. During this phase of the experiment, two groups of rats were pre-exposed to distal landmarks that surrounded the pool. For rats in group session, the relationship between the distal landmarks and the platform remained in constant position within each of the four trial blocks that were administered. For rats in group trial, however, the platform was moved to a new location on each trial, thus, ensuring that there was never a constant relationship between the distal landmarks and the submerged platform. Rats in group session-control and group trial-control received identical training to rats in group session and group trial, respectively, apart from the fact that a curtain surrounding the pool obscured the distal landmarks in both these control groups. In a second stage of the experiment, the submerged platform was placed in a novel location, and did not have a beacon attached to it. Consequently, rats had to learn this new location with respect to the distal landmark cues. During this stage of the experiment, rats in group session were faster to learn the novel platform location relative to group session control (see also Prados et al., 1999). In contrast, rats in group trial were slower to learn the new location relative to group trial control.

In order to account for these results, Redhead et al. (2001: see also Prados et al., 1999) appealed to attentional explanation. For group trial, the distal landmarks were never relevant for finding the platform during the pre-exposure trials and, consequently, the attention paid to these cues would diminish. In the second stage of the experiment, however, rats could only learn about the novel location with respect to these distal cues. The pre-exposure training for group trial, therefore, would serve to retard learning about the novel platform location, relative to a control group in which the distal landmarks were never made irrelevant (group trial control). For group session, in the first stage of the experiment, the distal landmarks signalled the platform location within each block of four pre-exposure trials. As these cues are relevant to finding the platform, attention to the distal landmarks would increase. During the second stage of the experiment, therefore, the pre-exposure training for group session would serve to facilitate learning, relative to a control group for which the landmarks were never made relevant (group session-control). Importantly, this attentional explanation is not consistent with the Miller-Shettleworth model because it assumes the salience of elements (α) to be fixed.

The Miller-Shettleworth model also struggles to account for the two published reports of an intradimensional-extradimensional (ID-ED) shift effect within the spatial literature. The simple form of an ID-ED experiment comprises two stages of training, and a set of stimuli drawn from two different dimensions (e.g. Mackintosh & Little, 1969). In the first stage, participants are trained that stimuli from one dimension are relevant to acquiring the outcome of the trial, while those from a second dimension are irrelevant. During the second stage of the experiment, novel stimuli from the dimensions used in stage one are presented. For participants undergoing an intradimensional (ID) shift, the same dimension remains relevant for the solution of the task, whereas for those undergoing an extradimensional shift (ED) the previously irrelevant dimension becomes relevant. The first report of an ID-ED effect in the spatial domain was reported by Trobalon, Miguelez, McLaren, and Mackintosh (2003), who trained rats in an ID group to receive food when they visited the western, but not the northern, arm of a radial maze. Rats in an ED group received food when they visited an arm of the maze textured with wood, but not plastic. In stage 2 of the experiment, all rats were rewarded for running down the south-west arm, but not the south-east arm, of the same maze. The results indicated that rats in the ID group solved the task more readily in stage 2 than did the rats in the ED group.

A second report of an ID-ED effect in the spatial domain has recently been reported by Cuell et al. (2012), who trained rats in a place group to find the location of a hidden goal with reference to the shape, and the extra-maze cues, of a distinctively-shaped water maze while laminated cards attached to the wall of the water maze were irrelevant. Rats in a landmark group were required to find the goal with reference to laminated cards that were attached to the walls of the water maze, while the distinctive shape of the arena and extra-maze cues were irrelevant. During a subsequent test stage, place cues were relevant for a new discrimination. The results indicated that the place cues better controlled searching for the goal in the place group, which had completed an intradimensional shift, relative to the landmark group, which had completed an extradimensional shift.

In their discussion of the ID-ED effect, both Mackintosh (1975, p. 279) and Le Pelley (2004, p. 212), argue that the observed retardation of learning during the second discrimination in ED groups, relative to ID groups, can only be explained by variations in the attention paid (α) to relevant or irrelevant stimuli. On this basis, it seems that the Miller-Shettleworth model is unable to provide an explanation for the ID-ED effects observed by Trobalon et al. (2003), and Cuell et al. (2012). The theory provided by Miller and Shettleworth (2007, 2008, 2013), however, focused specifically on how learning about spatial features, such as landmarks, interacts with geometry learning. To date, there has been no study which has examined whether the ID-ED effect persists in spatial navigation when landmarks and boundary shape alone (not place cues), are manipulated in such a way.

As the ID-ED shift procedure establishes one dimension as entirely irrelevant to the purpose of acquiring the goal, and a second dimension as fully predictive of the goal, the procedure is also ideal for testing theories that afford the shape of an environment a special status. As reviewed in Chapter 1, a number of theories propose that learning about the geometry, or boundary, of an environment will be unaffected by other highly relevant data, or predictive, cues (e.g. Cheng, 1986; Doeller & Burgess, 2008; Gallistel, 1990; Wang & Spelke, 2002, 2003). According to these analyses, even if the boundary shape of an environment is established as entirely irrelevant (and other cues as fully predictive) for navigation in stage 1 of the experiment, subsequent navigation based upon boundary shape in stage 2 should be unaffected. If this result were obtained, it would constitute particularly strong evidence for the modular basis of geometry in spatial navigation. In contrast, should the current experiments demonstrate superior learning in participants undergoing an ID shift, rather than an ED shift, then the modular analysis of geometry in navigation would be undermined. Furthermore, should an ID-ED effect be observed, it will be possible to make a more constrained theoretical interpretation of how landmarks and boundary geometry interact, as the ID-ED effect is widely acknowledged to indicate the effect of learned attentional changes to cues (e.g. Esber & Haselgrove, 2011; Le Pelley, 2004; Mackintosh, 1975). To avoid undue repetition, discussion of these theories is restricted to the general discussion of this chapter.

In the three ID-ED experiments reported here, participants were first trained that either landmarks or the geometric properties of the boundary of a distinctively-shaped arena were relevant to finding a hidden goal in stage one. In stage two, novel landmarks were presented in an arena of a different shape and participants completed either an ID, or an ED, shift from stage one. According to theories which suggest that learning about geometric information does not interact with learning about landmarks during navigation (e.g. Cheng, 1986), as well as Miller and Shettleworth's (2007, 2008, 2013) associative theory, performing an ED shift should have no effect on performance relative to the ID group. A slightly different pattern of predictions can be derived from the model of spatial navigation provided by Doeller and Burgess (2008), which states that learning about the boundaries of an environment occurs in an incidental manner. Consequently, training that establishes the shape of an environment as irrelevant to finding the goal in stage 1 should not retard subsequent learning about the boundary shape in stage 2, at least relative to training in which the shape of an environment was not irrelevant in stage 1. In contrast to learning about boundary information, learning about landmark cues is said to proceed in manner consistent with associative learning. It is important to note, however, that Doeller and Burgess (2008) do not specify which associative theory governs landmark learning. If it assumed that learning about landmarks is governed by the Miller-Shettleworth model, then training that establishes landmarks as irrelevant to finding the goal in stage 1 should not retard subsequent learning about the novel landmarks presented in stage 2. In contrast, if learning about landmarks is governed by the associative model proposed by Mackintosh (1975), then training that establishes landmarks as irrelevant to finding the goal in stage 1 would be expected to produce retarded learning about landmarks in stage 2, again, relative to training in which landmarks have never been irrelevant.

3.1 Experiment 4

In stage one, participants were trained to find a hidden goal that, on each trial, was always located in one of the four corners of a kite-shaped arena, each of which was coloured a different shade of blue. From this point on, the landmarks created by the shading of the corners of the walls are referred to as wall panels. The positions of these wall panels changed to different corners on each trial. For half the participants in stage 1, the hidden goal could only be located with reference to information provided by the shape of the arena, thus, information provided by the landmarks was irrelevant. For example, the goal might always be hidden at the most acute corner of the kite, the colour of which changed on a trial by trial basis. For the remainder of the participants, the hidden goal could only be located with reference to one of the four wall panels, thus, information provided by the shape of the arena was irrelevant to finding its specific location. For example, the goal might always be hidden in the corner that was the darkest shade of blue, irrespective of which corner this shade was located.

In stage two of the experiment, participants had to learn to find a hidden goal in a trapezium-shaped arena, the corners of which were four different shades of red. As before, the positions of the landmarks changed to different corners on each trial. During stage two, participants who completed an ID shift had to learn about a cue from the same dimension that was relevant to finding the goal in stage one. Consequently, if the shape of the arena was relevant to finding the goal in stage one, then it was also relevant to finding the goal in stage two (group shape-shape). Likewise, if landmarks were relevant to finding the hidden goal in stage one, then they were also relevant to finding the goal in stage two (group landmark-landmark). Participants who completed an ED shift, however, had to learn in stage 2 about a cue from the dimension that was irrelevant to finding the goal in stage one. Consequently, participants who had learned the location of the goal with respect to the shape of the arena in stage one had to learn the location of the goal with respect to landmarks in stage two (group shape-landmark), and participants who had learned the location of the goal with respect to landmarks in stage one had to learn the location of the goal with respect to the shape of the arena in stage two (group landmark-shape). To assess navigational behaviour over the course of the experiment, the time taken to find the hidden goal was recorded on each trial.

3.1.1 Method

3.1.1.1 Participants

48 participants were recruited from the University of Nottingham (31 female). Participants were randomly allocated to one of the four groups in the experiment, and were given course credit or £5 in return for participation. The age of participants ranged from 18 to 28 years (mean = 19.31, *SD* = 1.90). An additional £10 was awarded to the participant who completed the experiment in the shortest time.

3.1.1.2 Materials

Mazesuite software (Ayaz et al., 2008; www.mazesuite.com) was, again, used to construct and display the virtual environments used in this experiment, which was displayed using the same computer and screen as Experiment 1. The kite- and trapezium-shaped environments used in this experiment were built from the same cream coloured walls defined in Experiment 1. In keeping with Experiment 1, both arenas also had a grass texture applied to the floor, and were viewed from a first-person perspective. Assuming a walking speed similar to that in the real world (2 m/s), the perimeter of the trapezium-shaped arena was 63m, with the smallest wall being 9m, the largest wall 27m, and the remaining two walls 13.5m in length. The isosceles trapezium was configured such that it contained angles of 48.19º and 131.81°. The dimensions of the kite-shaped arena were identical to those reported in Experiment 1. Four pairs of coloured wall panels, each 1.13 m in length and 2.5m in height, served as landmarks, and were located on either side of each corner in an arena (see Figure 3.1).

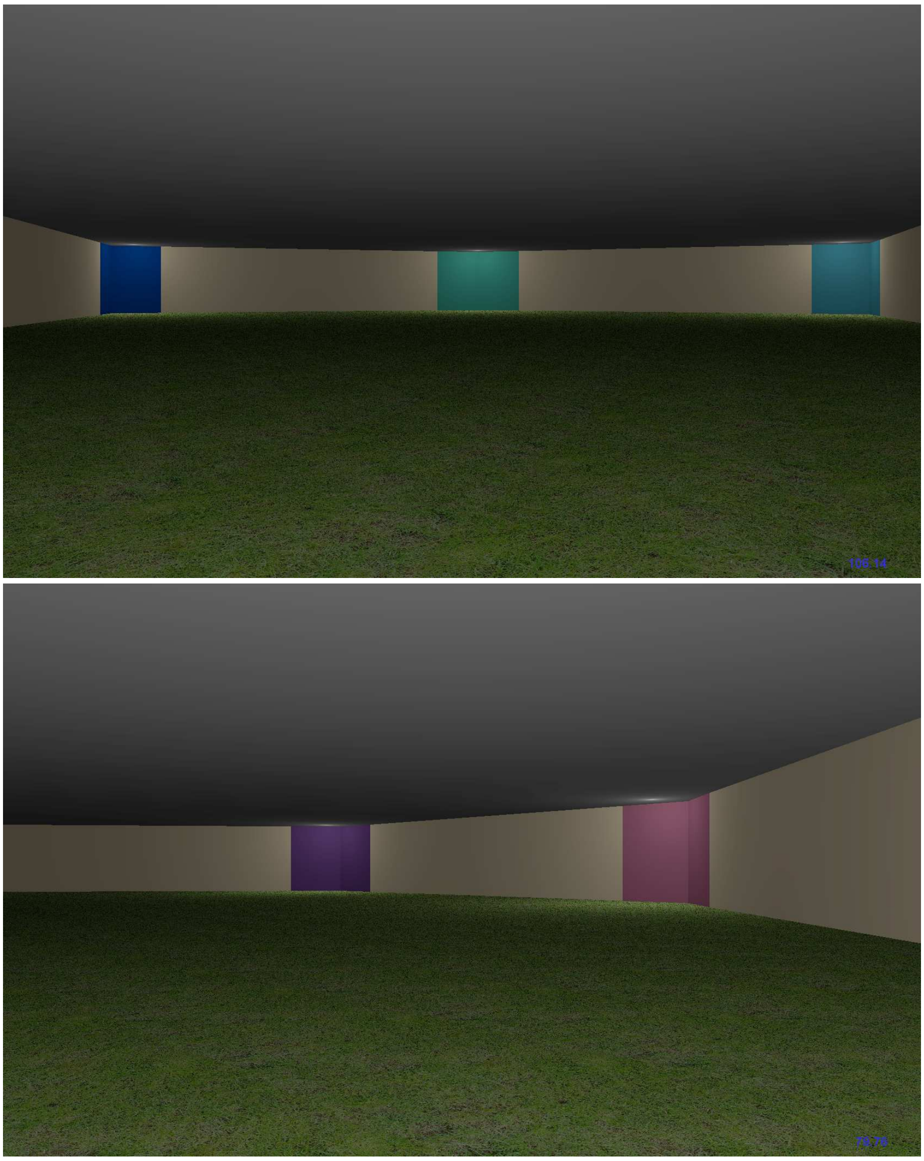


Figure 3.1. Examples of the kite-shaped (top), and trapezium-shaped arenas used in Experiment 4.

The four blue wall panels presented in the kite-shaped arena were defined as RGB; 25, 127, 102; 25, 102, 127; 0, 25, 102 and 51, 102, 204, and the four red wall panels presented in the trapezium-shaped arena were; 127, 25, 51; 127, 51, 76; 10, 25, 102 and 51, 25, 76. As with Experiment 1, the goals within both kite- and trapezium-shaped arenas were 1.08m x 1.08m square-shaped regions. In the current experiment, however, the goals were located 1.48m away from the walls of the arena, along on a notional line that bisected the corner. It was necessary to move the goals closer to corners of the environment, compared to Experiment 1, so that the landmark cues that were used in Experiment 5 did not obscure the view of the corner of the environment when participants found the hidden goal. Finally, an exploration arena, identical to one detailed in Experiment 1, was again used in this experiment to allow participants to become familiar with the controls of the experimental task.

3.1.1.3 Procedure

After signing a standard consent form, participants were given the following set of instructions on paper:

This study is assessing human navigation using a computer generated virtual environment. During this experiment, you will complete 48 trials. In each trial, you will be placed into a room that contains an invisible column. Your aim is to end the trials as quickly as possible by walking into the column.

You will view the environment from a first person perspective, and be able to walk into the column from any direction using the cursor keys on the keyboard. Once you've found the column a congratulatory message will be displayed and you should hit enter when you're ready to begin the next trial.

You will always be in the centre of the arena when a trial begins, but the direction in which you face at the start of each trial will change.

To start with, you may find the column is difficult to find. There is, however, a way of learning exactly where the invisible column will be on each trial. It's a good idea to fully explore the environment on the first few trials, this will help you to learn where the column is going to be.

This session should take around 30-40 minutes. If at any point you wish to stop this session, please notify the experimenter and you'll be free to leave without having to give a reason why. Your results will be saved under an anonymous code, and kept confidential throughout.

The person who takes the least time to complete this experiment will win a £10 prize!

Participants sat not more than 100 cm from the screen, and controlled navigation using the keyboard in the same manner as described in Experiment 1. Participants were, again, provided with the opportunity to move around the octagonal exploration arena for two 30 second trials before beginning the first experimental trial. In the kite-shaped arena, participants again began each trial at a point located halfway between the apex and obtuse corners and, in the trapezium-shaped arena, at a point half way along a notional line from the centre of the shortest wall to the centre of the longest wall. The direction in which participants began facing was randomised for every trial.

Generating every possible configuration of four landmarks in the four corners of the arenas produced 24 different trials for both the kite- and the trapezium-shaped arenas. Each of these arenas was presented once to each participant, the order of which was randomized for each participant independently. Participants were first required to complete 24 trials in the kite-shaped arena (stage 1), before completing 24 trials in the trapezium-shaped arena (stage 2). On each trial, participants were required to find the hidden goal by using the four cursor keys as described above. There was no time limit for any trials, thus, each trial ended only when the hidden goal was found. Once the hidden goal had been found, participants could no longer move within the arena and a congratulatory message (*Congratulations, you found the goal!*) was displayed on screen.

During stage 1 for participants in groups shape-shape and shape-landmark, and during stage 2 for participants in groups shape-shape and landmark-shape, the goal was located in the same corner of the arena on each trial. Each of the 4 wall panels was located in the goal corner on 6 trials, and in non-goal locations on the remaining 18 trials. During stage 1 for participants in groups landmark-landmark and landmark-shape, and during stage 2 for participants in groups landmark-landmark and shape-landmark, the goal was located adjacent to the same wall panel on each trial. Each of the 4 corners contained the goal on 6 trials, and did not contain the goal on the remaining 18 trials.

Full details of stage 1 and stage 2 counterbalancing are given in Figure 3.2. Attention should, however, be paid to the counterbalancing employed for group shape-shape, which was arranged such that any direct transfer of local geometric cues from the kite to the trapezium would not aid performance. For

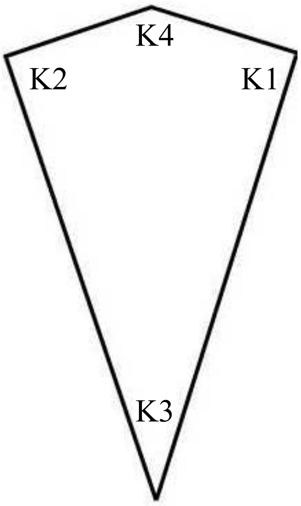
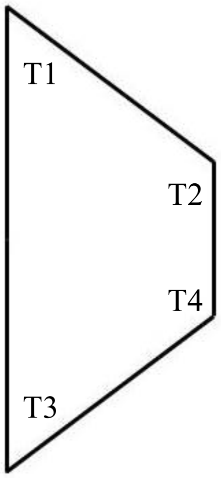
Group	Stage 1	Stage 2	Arena corners
Shape-Shape	K1	T1	
	K1	T2	
	K2	T3	
	K2	T4	
	K3	T2	
	K3	T4	
	K4	T1	
	K4	T3	
Landmark-Landmark	B1	R1	
	B1	R3	
	B2	R2	
	B2	R4	
	B3	R1	
	B3	R3	
	B4	R2	
	B4	R4	
Landmark-Shape	B1	T4	
	B1	T1	
	B2	T2	
	B2	T3	
	B3	T4	
	B3	T1	
	B4	T2	
	B4	T3	
Shape-Landmark	K1	R1	
	K1	R3	
	K2	R2	
	K2	R4	
	K3	R1	
	K3	R3	
	K4	R2	
	K4	R4	

Figure 3.2. Complete counterbalancing details for Experiments 4, 5, and 6 where K1, K2, K3, K4 represent corners of the kite, T1, T2, T3, T4 represent corners of the trapezium, B1, B2, B3, B4 represent the blue landmarks present in the kite-shaped arena, and R1, R2, R3, R4 represent the red landmarks present in the trapezium-shaped arena.

instance, if the goal in the kite was located in a corner where the right wall was long and the left wall was short, the goal position in the trapezium would always be located where the left wall was longer than the right wall. Similarly, if the goal location in the kite was in the acute or obtuse angled corners, then in the trapezium the goal would be located in an obtuse or acute angled corner, respectively.

3.1.2 Results

3.1.2.1 Stage 1

Figure 3.3 shows the latency, in seconds, from the beginning of each trial to enter the region defined as the hidden goal for the four groups during the 24 trials of stage 1 of the experiment. The mean latencies in the four groups decreased across this stage of the experiment, but there was little indication of any differences between the groups. A two-way ANOVA of individual latencies, with the between-subject variable of relevant cue in stage one (landmarks or shape), and within-subject variable of trial (1-24), revealed a significant main effect of trial, $F(23, 1058) = 55.55$, $MSE = 212.55$, $p < .001$, $\eta_p^2 = .54$, reflecting that the latency to find the goal decreased over trials. There was no main effect of relevant cue $F(1, 46) = 1.05$, $MSE = 751.87$, $p = .31$, $\eta_p^2 = .02$, however, there was a significant interaction between trial and relevant cue, $F(23, 1058) = 1.72$, $MSE = 212.55$, $p = .02$, $\eta_p^2 = .034$. Simple main effects analysis revealed shorter latencies to find the goal in the landmark-relevant, than in the shape-relevant groups on trial 1, but the reverse pattern on trial 3, $Fs(1, 1104) > 7.86$, $MSE = 235.02$, $ps < .005$, $\eta_p^2 > .007$.

However, no significant differences in performance were noted by the end of stage 1.

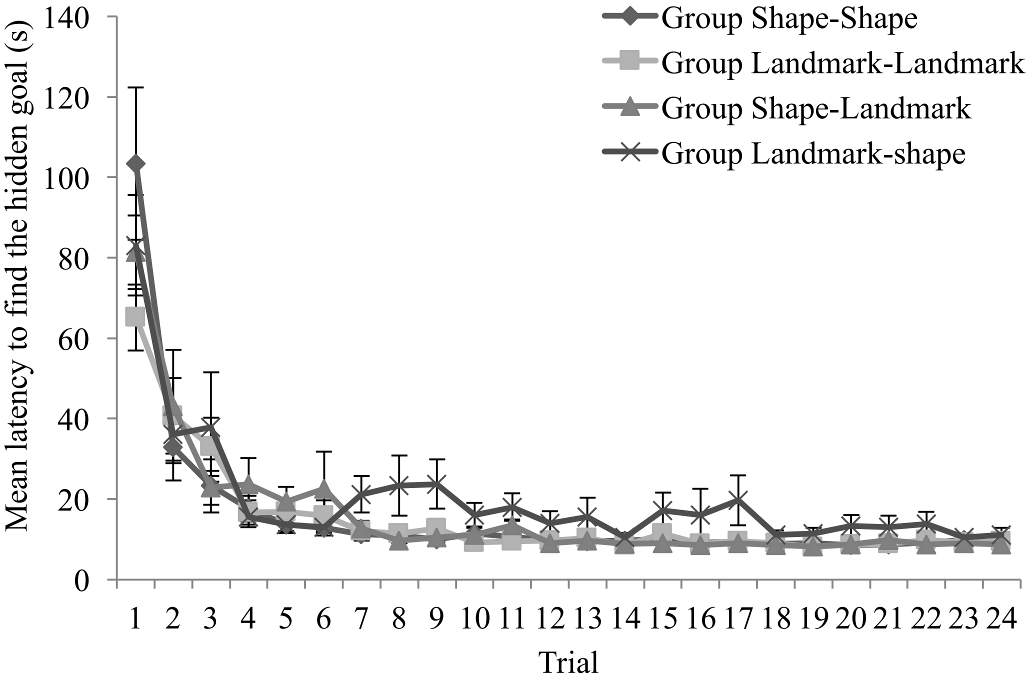
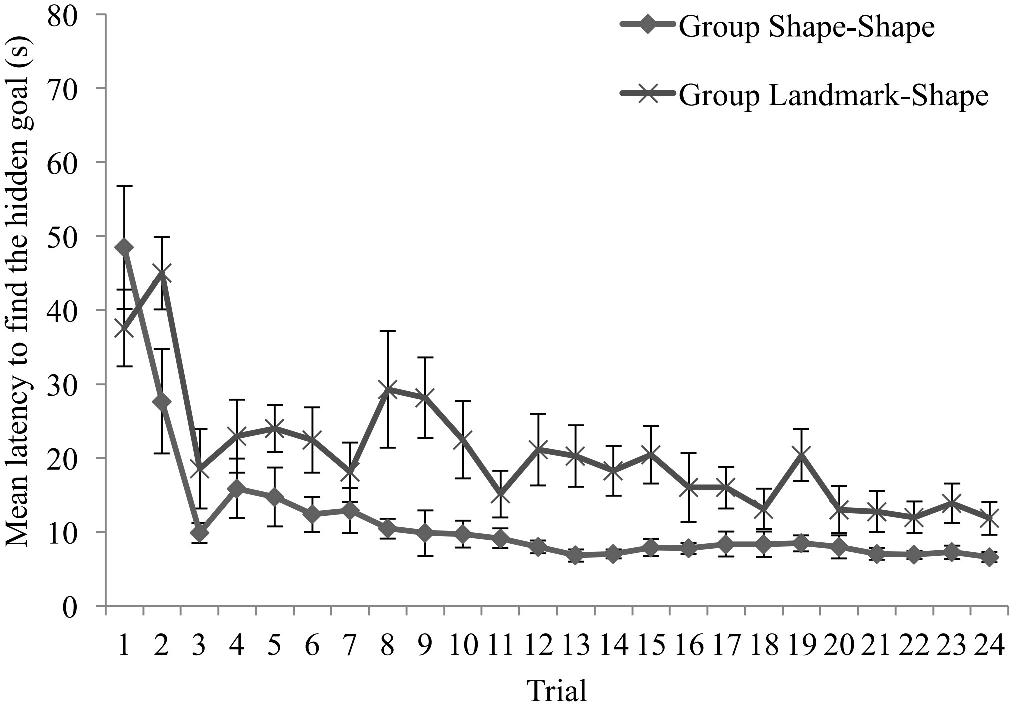


Figure 3.3. Mean latencies of the four groups to find the hidden goal in stage 1 of Experiment 4. Error bars show 1 +/- standard error of the mean.

3.1.2.2 Stage 2

The mean latencies, in seconds, to find the goal during stage 2 are shown in the top panel of Figure 3.4 for groups shape-shape and landmark-shape, and in the bottom panel of Figure 3.4 for groups landmark-landmark and shape-landmark. It can be seen that both groups that performed an ED shift (groups landmark-shape and shape-landmark) showed longer latencies to find the goal relative to the appropriate ID groups (groups shape-shape and landmark-landmark). A three-way ANOVA of individual latencies to find the goal, with the between-subject variables of shift (ID or ED) and relevant cue



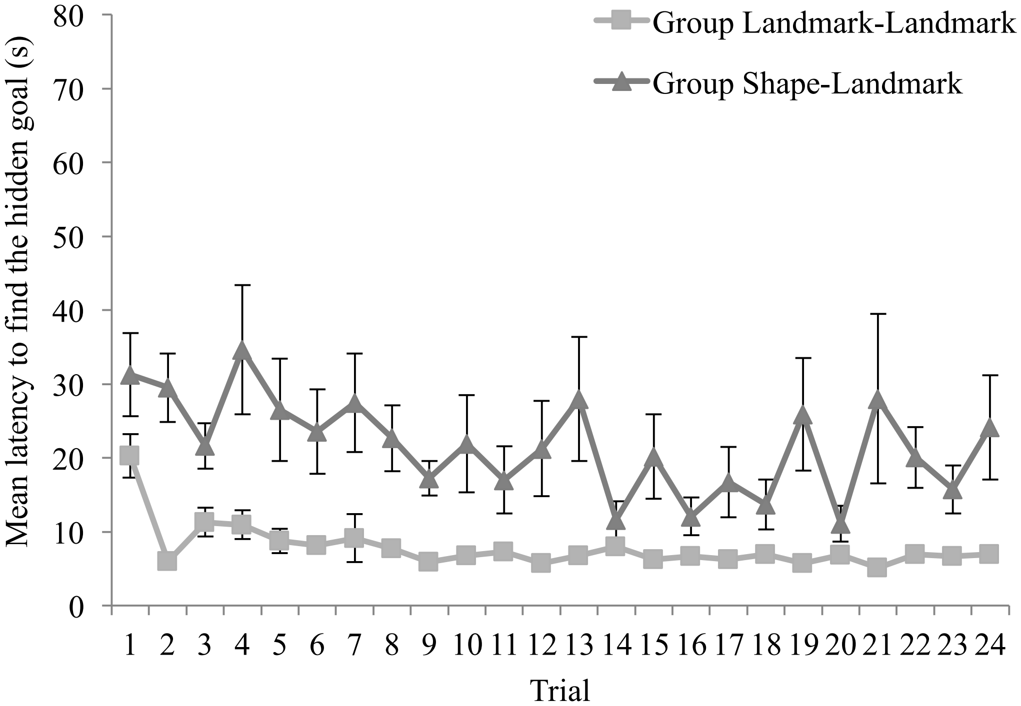


Figure 3.4. Top: Mean latencies of groups shape-shape and landmark-shape to find the hidden goal in stage 2 of Experiment 4. Bottom: Mean latencies of groups shape-landmark and landmark-landmark to find the hidden goal in stage 2 of Experiment 4. Error bars show 1 +/- standard error of the mean.

in stage two (shape or landmarks), and within-subject variable of trial (1-24), revealed a significant main effect of trial $F(23, 1012) = 9.65$, $MSE = 155.94$, $p < .001$, $\eta_p^2 = .18$, of shift, $F(1, 44) = 43.12$, $MSE = 871.22$, $p < .001$, $\eta_p^2 = .49$ but no effect of relevant cue $F<1$. Crucially, there was a significant interaction between shift and trial, $F(23, 1012) = 1.71$, $MSE = 155.94$, $p = .02$, $\eta_p^2 = .04$. Simple effects analysis of this interaction revealed that the ED shift groups, overall, were significantly slower to find the goal than the ID shift groups on trials 2-13, 15, 17, 19, and 21-24, $F\text{s}(1, 1056) > 3.961$, $MSE = 185.75$, $ps<.047$, $\eta_p^2 > .004$. There was not a significant interaction between shift and relevant cue $F(1, 44) = 2.12$, $MSE = 871.22$, $p = .15$, $\eta_p^2 = .046$, however, the interaction between relevant cue and trial was significant, $F(23, 1012) = 2.84$, $MSE = 155.94$, $p < .001$, $\eta_p^2 = .02$. Simple main effects analysis revealed that participants who were navigating on the basis of landmarks were significantly quicker at finding the goal on trials 1 and 2 than participants navigating in the basis of shape, $F\text{s}(1, 1056) > 19.16$, $MSE =185.75$, $p\text{s} < .001$, $\eta_p^2 > .01$. The three-way interaction was not significant $F(23, 1012) = 1.06$, $MSE = 155.94$, $p = .39$, $\eta_p^2 = .02$.

3.1.3 Discussion

Establishing either landmarks or the geometry of the environment as relevant to navigation influences the speed at which novel stimuli drawn from these stimulus dimensions are subsequently learned about. Specifically: (1) When landmarks have successfully guided navigation in the past then subsequent navigation using information provided by the geometry of the arena is retarded relative to a group who initially navigated using geometry.

(2) When information provided by the geometry of the arena has successfully guided navigation in the past then subsequent navigation using landmarks is retarded relative to a group who initially navigated using landmarks. Results (1) and (2) are difficult to reconcile with Miller and Shettleworth's (2007; 2008, 2013) associative theory of spatial learning, which proposes that attention paid to navigational elements is fixed; thus, precluding it from explaining any demonstration of a spatial ID-ED effect. These results are also inconsistent with Cheng's (1986) modular analysis of spatial learning, which proposes that geometric information is encoded in a module that cannot be influenced by learning about landmarks (see also Gallistel, 1990; Wang & Spelke, 2002, 2003). Finally, result (1) is difficult to reconcile with the proposals of Doeller & Burgess (2008), who suggested that learning about the boundary of the environment is impervious to the influence of learning about information from landmark information and, importantly, that learning relative to boundaries occurs independent of behavioural error.

The stimuli employed as landmarks in Experiment 4 were coloured panels that were spatially integrated into the boundaries of the arenas during stages 1 and 2. This choice of stimuli has a number of theoretical implications, two of which will be considered now. First, it has been suggested that learning may result in the acquisition of orienting responses to cues that are important to the solution of a discrimination (Spence, 1940, 1952). If these cues are subsequently established as unimportant to the solution of a discrimination (as in the case of an ED shift) then acquisition will be retarded because orienting responses will be made to the (now) irrelevant cue, potentially hindering the perception of the relevant cue. This analysis shifts the locus of the effect of the

ID-ED shift to a more peripheral orienting mechanism than the analysis of the effect provided by theories of learning such as Mackintosh's (1975), which assumes the effect is the consequence of a more central change in the attention that is paid to a stimulus despite it being perceived. By demonstrating, here, an ID-ED effect when the features of the arena relevant to finding the goal are spatially integrated with the features of the arenas that are irrelevant makes it unlikely that the current results were a consequence of a more peripheral strategy (cf. Pearce, Esber, George, & Haselgrove, 2008). Second, although coloured wall panels have been considered as landmarks by some authors (e.g. Pearce et al., 2006), it seems entirely reasonable to argue that such features are integral components of the boundary of the arena (e.g. Wilson & Alexander, 2010). If this is accepted, then it may be argued that Experiment 4 only goes so far as to demonstrate that information contained within a geometric module is able to interact, a possibility that is not entirely ruled out by analyses such as those proposed by Cheng (1986) and Doeller and Burgess (2008). Experiment 5 was, therefore, conducted to address this matter, and examined whether discrete landmarks that are spatially separated from the arena boundary can influence navigation that is based on information that is provided by its shape (and vice versa).

3.2 Experiment 5

Experiment 5 replicated the design of Experiment 4, but in place of coloured wall panels, coloured spheres that were present in each corner of an arena served as landmarks. The spheres were spatially separated from the boundaries of the environment, such that in a horizontal plane the full 360 degrees of the sphere could be viewed, and were suspended at a height that enabled participants to walk under them. In stage 1, four spherical landmarks of different shades of blue, were located in the four corners of the kite-shaped arena used in Experiment 4. In stage 2, four spherical landmarks of different shades of red, were located in the four corners of the trapezium-shaped arena used in Experiment 4. For group shape-shape the hidden goal was again always located in the same corner of the kite, and the same corner of the trapezium, no matter which landmark was present in that corner in either arena. For group landmark-landmark, the goal was always under the same landmark in the kite or trapezium, no matter which corner the landmark occupied in each arena. For group shape-landmark, the hidden goal remained in the same corner of the kite no matter what landmark was present in the corner, but in the trapezium the goal then remained under the same landmark no matter which corner it was in. Finally, for group landmark-shape, the hidden goal remained under the same landmark in the kite-shaped arena no matter which corner the landmark was in, but in the trapezium remained in one corner no matter which landmark was present in that corner.

3.2.1 Method

3.2.1.1 Participants

32 participants were recruited from the University of Nottingham (24 female). Participants were again randomly allocated to one of the four groups in the experiment, and were given course credit or £5 in return for participation. The age of participants ranged from 18 to 37 years (mean =

21.18, *SD* = 4.73). An additional £10 was awarded to the participant who completed the experiment in the shortest time.

3.2.1.2 Materials

The monitor, computer equipment, and all arenas were exactly the same as those used in Experiment 4, with the exception of the landmarks which, for the current experiment, were discrete spheres 90 cm in diameter instead of coloured wall panels (see Figure 3.5). The spherical landmarks were constructed using Blender software (www.blender.org) and imported into Mazesuite. The blue spheres used in stage 1 of the experiment were defined as RGB; 0.000, 0.540, 0.640; 0.159, 0.326, 0.800; 0.000, 0.123, 0.720 and 0.000, 0.464, 0.800, and the red spheres used in stage 2 as; 0.635, 0.239, 0.640; 0.640, 0.000, 0.392; 0.512, 0.000, 0.314 and 0.238, 0.131, 0.465. Within the arenas, the landmarks were 1.48m away from the apex of each corner, on a notional line that bisected the corner. The walls of both the kite-shaped and trapezium-shaped arenas were a uniform cream colour throughout the experiment.

3.2.1.3 Procedure

The procedure for Experiment 5 was identical to Experiment 4.

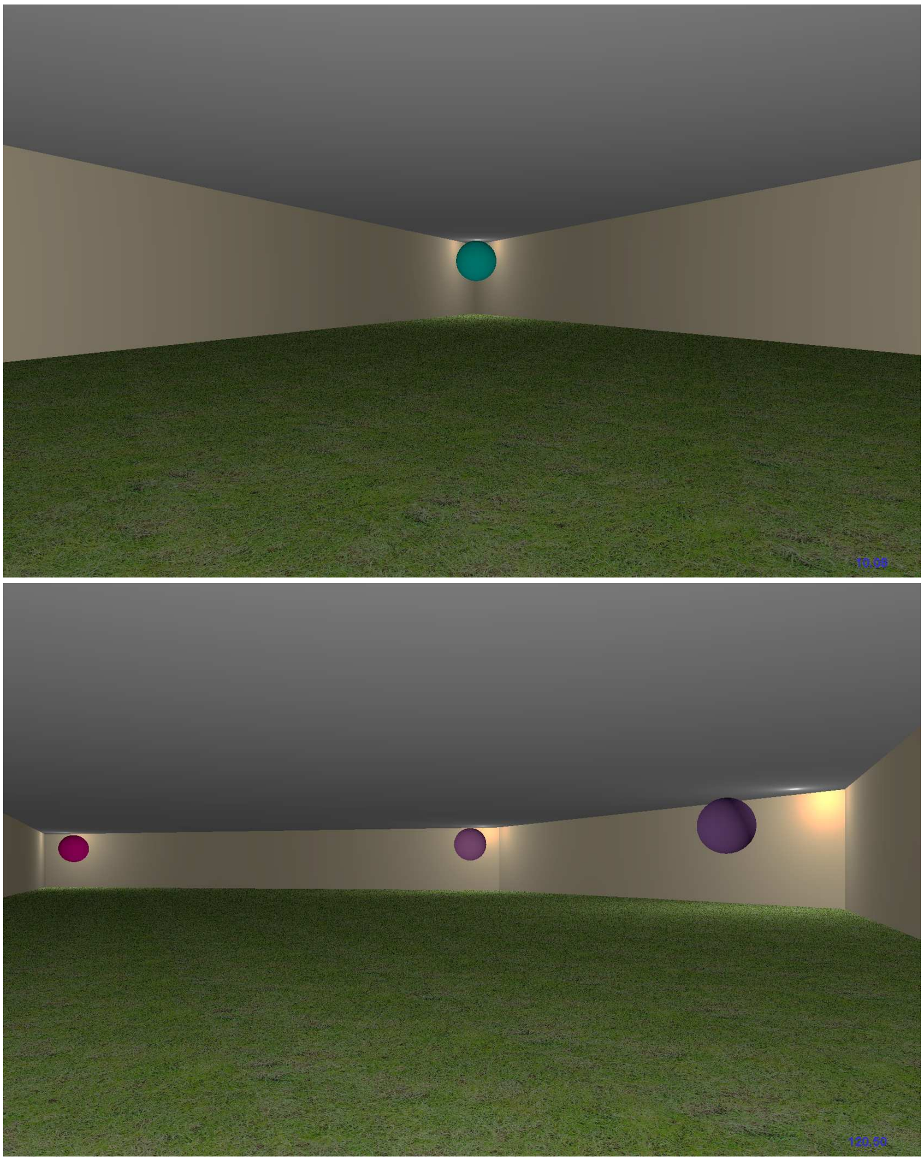


Figure 3.5. Examples of the kite-shaped (top), and trapezium-shaped (bottom) environments used in Experiments 5 and 6.

3.2.2 Results

3.2.2.1 Stage 1

Figure 3.6 shows the mean latency of the 4 groups to find the hidden goal during the 24 trials of stage 1. In keeping with the results of Experiment 4, learning progressed at a similar rate in the four groups and the asymptotes of performance were similar. A two-way ANOVA of individual latencies to find the goal, with a between-subject variable of relevant cue in stage one (landmarks or shape), and a within-subject variable of trial (1-24), revealed a significant main effect of trial, $F(23, 690) = 26.11$, $MSE = 139.05$, $p< .001$, $\eta_p^2 = .47$. There was no main effect of relevant cue, $F(1, 30) = 2.20$, $MSE = 727.87$, $p= .15$, $\eta_p^2 = .07$, and no significant interaction between relevant cue and trial, $F<1$.

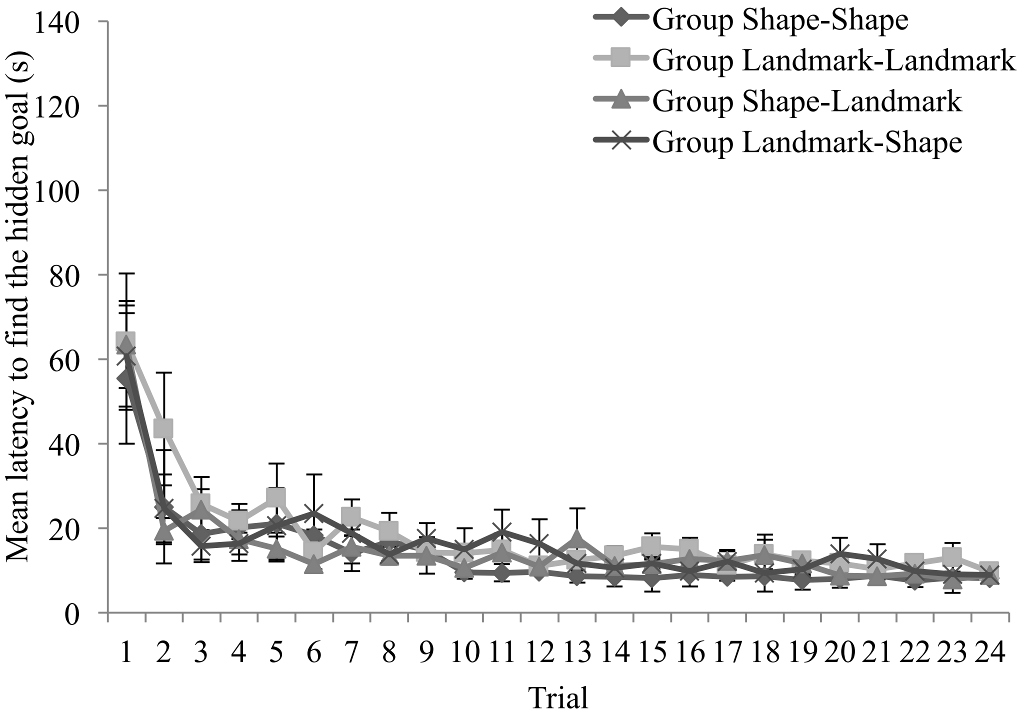
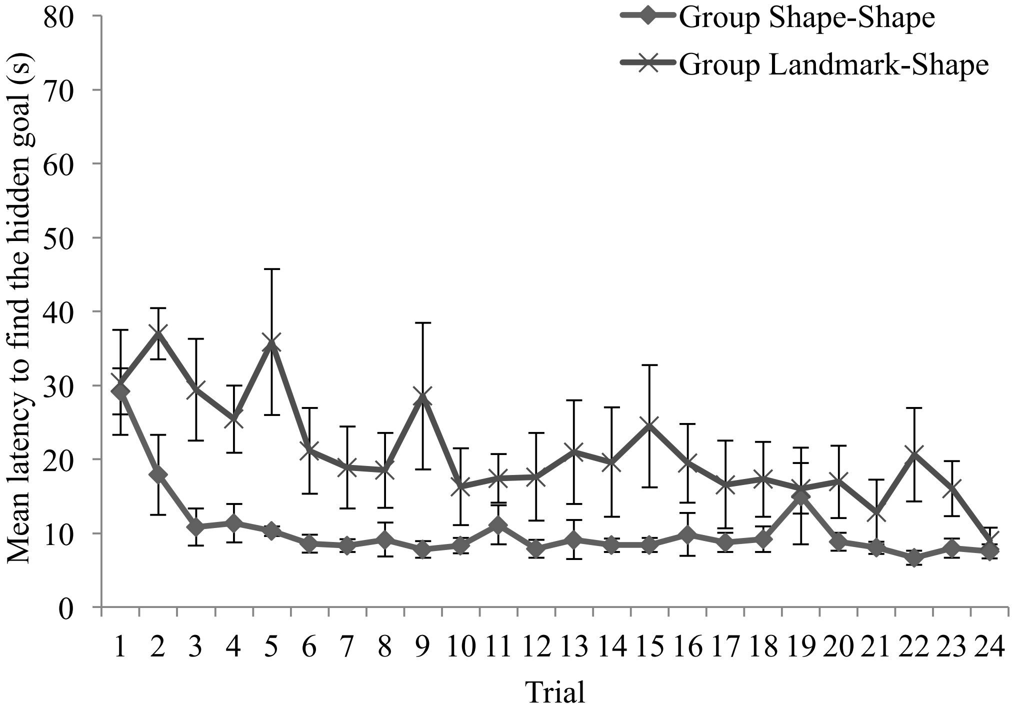


Figure 3.6. Mean latencies of the four groups to find the hidden goal in stage 1 of Experiment 5. Error bars show 1 +/- standard error of the mean.

3.2.2.2 Stage 2

The mean latencies, in seconds, to find the goal during stage 2 are shown in the top panel of Figure 3.7 for groups shape-shape and landmark-shape, and in the bottom panel of Figure 3.7 for groups landmark-landmark and shape-landmark. In keeping with the results of Experiment 4, both groups that performed an ED shift (groups landmark-shape and shape-landmark) showed longer latencies to find the goal relative to the appropriate ID groups (groups shape-shape and landmark-landmark, respectively). There was an indication that this effect was more sustained in the groups undergoing shape relevance training in stage 2 than groups who were undergoing landmark relevance training in stage 2. A three-way ANOVA of individual latencies to find the goal, with the between-subjects variables of shift (ID or ED) and relevant cue in stage two (shape or landmarks), and a within-subjects variable of trial (1-24), revealed a significant main effect of trial, $F(23,644) = 12.70$, $MSE = 76.72$, $p<.001$ $\eta_p^2 = .31$, and a significant main effect of shift, $F(1, 28) = 10.92$, $MSE = 968.61$, $p= .003$, $\eta_p^2 = .28$, confirming that those performing an ED shift were, overall, slower to find the goal than those performing an ID shift. The main effect of relevant cue approached significance, $F(1, 28) = 3.69$, $MSE = 968.61$, $p= .065$, $\eta_p^2 = .12$, which indicated that there was a trend towards participants finding the goal quicker when landmarks were relevant compared to when shape was relevant. Importantly, a significant interaction between shift and trial was obtained, $F(23, 644) = 3.13$, $MSE =76.72$, $p< .001$, $\eta_p^2 = .10$ Simple main effects analysis revealed that participants performing an ED shift were significantly slower to find the goal than participants performing an ID shift on trials 2-9, Fs$(1, 672) > 5.035$, $MSE = 11.89$, ps$< .025$, $\eta_p^2 > .01$. The interaction between relevant cue and shift was not significant, $F(1, 28) = 2.18$, $MSE = 968.61$, $p= .15$, $\eta_p^2 = .07$, nor was the interaction between relevant cue and trial interaction, $F(23, 644) = 1.43$, $MSE = 76.72$, $p= .09$, $\eta_p^2 = .05$. Finally, the three-way interaction was not significant, $F<1$.



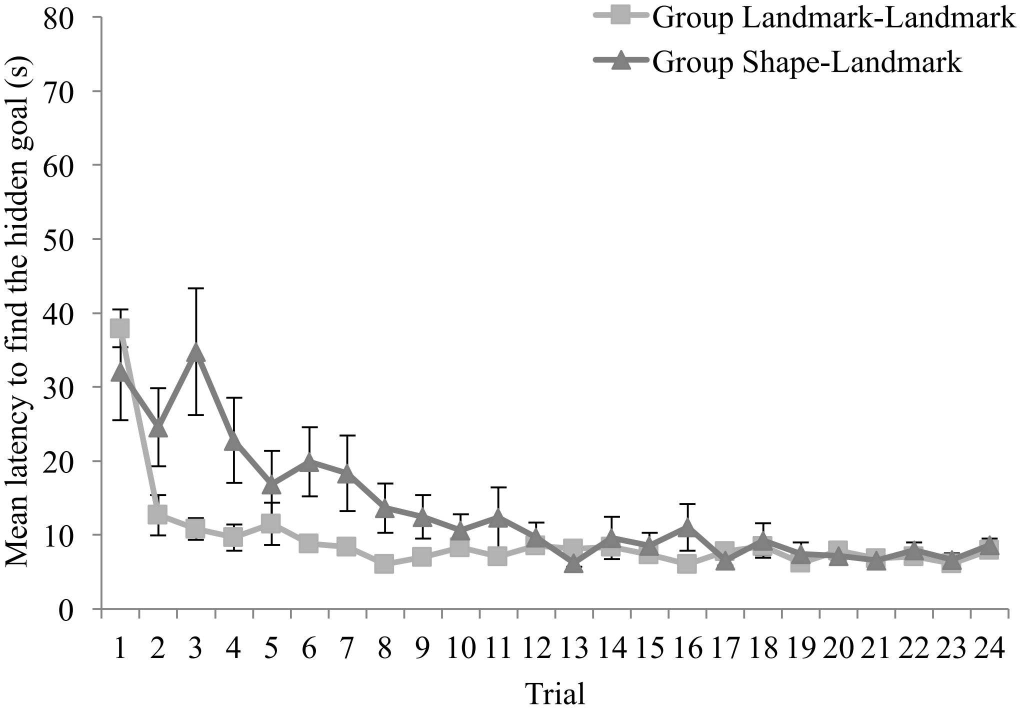


Figure 3.7. Top: Mean latencies of groups shape-shape and landmark-shape to find the hidden goal in stage 2 of Experiment 5. Bottom: mean latencies of groups shape-landmark and landmark-landmark to find the hidden goal in stage 2 of Experiment 5. Error bars show 1 +/- standard error of the mean.

3.2.3 Discussion

The results of Experiment 5 replicate and extend the generality of the results from Experiment 4: participants were slower to find a hidden goal when the cues relevant to navigation were from a dimension that had previously been irrelevant, rather than relevant, for navigation. Experiment 5 used intra-arena stimuli that were spatially separated from the arena boundary as landmarks, instead of the coloured wall-panels employed in Experiment 4. Consequently, it is difficult to argue that these stimuli were encoded by participants as boundary information. It seems, therefore, that the current experiment constitutes a demonstration that learning about a landmark interfered with learning about the geometric properties of an arena. These results are, thus, inconsistent with theories that suggest boundary cues have a special status, in that learning to them does not follow general associative principles of behavioural error and are not susceptible to interference from landmark information (e.g. Doeller & Burgess, 2008), or theories that emphasize a similar special status for geometric information (e.g. Cheng, 1986; Gallistel, 1990; Wang & Spelke, 2002, 2003). As with Experiment 4, the Miller-Shettleworth associative model of spatial navigation is precluded from explaining the ID-ED effect as it assumes that the attention paid to stimuli is not modifiable.

The retardation of navigation observed in the two ED groups (groups landmark-shape and shape-landmark) was, of course, a retardation relative to navigation in the two ID groups (groups shape-shape and landmark-landmark). It is conceivable, therefore, that the results of Experiment 4 and 5 do not reflect a retardation of learning in the ED groups. In keeping with the proposals of modular theories of geometric navigation (e.g. Cheng, 1986), it is possible that navigation in the two ED groups in stage 2 was, in fact, unaffected by navigation in stage 1. The difference observed between the ID and ED groups could, instead, reflect a facilitation of learning in the two ID groups – a possibility that is not explicitly prohibited by the aforementioned theories. This analysis encounters difficulty when explaining exactly why navigation should be facilitated in group shape-shape. The geometric cues of the goal location in stage 1 were deliberately chosen so as to not convey any advantage to participants when they moved to stage 2 of the experiment. If the goal was in an acute (or obtuse) corner in stage 1, then it was located in an obtuse (or acute) corner in stage 2. Similarly, if the goal was located, for example, in a corner that had a short wall to the left of a long wall in stage 1, then it was located in a corner that had a long wall to the left of a short wall in stage 2. Consequently, any direct transfer of geometric information pertaining to the goal location from stage 1 to stage 2 would hinder, rather than facilitate, navigation.

For Experiment 4, the landmarks were spatially integrated into the corners of the arena boundary whereas, in the current experiment, the landmarks were displaced from the arena boundaries. The results of Experiment 5 would, therefore, seem to be open to the peripheral orienting account described in the discussion of Experiment 4. Although it is not possible to fully rule out this analysis for Experiment 5, the landmarks were located sufficiently close to the corners of the arena that any orienting response made towards a landmark cue coincided with an orienting response toward the geometry of the corner that the landmark occupies. Similarly, any orienting response made towards a given corner of the arena will coincide with an orienting response towards the landmark placed in that corner. On this basis, it seems unlikely that peripheral orienting mechanisms provide an adequate explanation of the pattern of results observed.

3.3 Experiments 6a and 6b

At face value, Experiment 5 seems to constitute a challenge to theories of navigation that confer a special status to the global-shape of the environment. Experiment 5, however, failed to provide any evidence that, as a consequence of navigation, participants acquired a global representation of shape of the arena. As cognitive map theories (e.g. Cheng, 1986; Gallistel, 1990; O'Keefe & Nadel, 1978) predict that such a representation will be extracted as a consequence of navigation, it is difficult to know how much of a challenge Experiment 5 poses to these theories. These experiments, perhaps, only challenge the Miller-Shettleworth model of spatial navigation. This issue is particularly important when one considers the results of spatial learning experiments conducted with rats, which provide evidence for a local encoding of geometry.

As reviewed in Chapter 1, Pearce et al. (2004) demonstrated that, having been trained to navigate to a particular corner of a kite-shaped arena, rats preferentially searched in the corners of a rectangle-shaped arena that contained the same local geometric cues (see also: Lew et al., 2014; McGregor et al., 2006; Pearce et al., 2004; Tommasi & Polli, 2004). On the basis of this behaviour, it has been suggested that organisms use local geometric cues to guide navigation. These results, however, do not rule out the possibility that, in addition to the encoding of local-shape information, rats also encoded global-shape information that was unique to the rectangle-shaped arena. By the same token, any experiment that is claimed to constitute a challenge to the assumptions of theories of navigation which assume the presence of a global-shape representation should also provide evidence for such a global representation - evidence which Experiments 4 and 5 (as well as other related cue competition experiments; e.g. Pearce et al., 2006) are lacking.

Experiments 6a and 6b sought to replicate the findings of Experiment 5, in addition to assessing whether participants formed any knowledge of the global-shape of the arena and, more importantly, whether this information was influenced by the relevance training provided by the ID-ED task. Experiment 6a was an exact replication of Experiment 5, but with the addition, at the end of the experiment, of a shape recognition task. Experiment 6b was a close replication of Experiment 5, except that the participants began by navigating in the trapezium-shaped arena in stage 1, following which participants navigated in the kite-shaped arena during stage 2. The shape recognition task was also administered at the end of Experiment 6b. For the shape-recognition task at the end of Experiments 6a and 6b, participants were presented with black and white “target” pictures of a kite and a trapezium and “distracter” stimuli, similar in form to the targets (a triangle and a parallelogram, respectively). Participants were required to report whether, or not, the shapes presented matched those explored during the preceding navigation stages. If the training in stages 1 and 2 of this experiment permitted participants to extract a global, allocentric, representation of the shapes of the kite- and trapezium-shaped arenas, then they should be able to distinguish these targets from the distracters. This being the case, it would provide evidence for the presence of global encoding of the shape of the arena as a consequence of exploration within it. At the same time, if performance on this recognition task were influenced by relevance training with landmarks, this would constitute evidence that a global representation of shape is susceptible to interference from local landmarks – a possibility that, as outlined earlier, is prohibited by a variety of theories of spatial navigation (e.g. Cheng, 1986; Doeller & Burgess, 2008, Gallistel, 1990).

3.3.1 Method

All procedural, material, and apparatus details for the navigation stages of Experiment 6a were identical to those reported in Experiment 5. Experiment 6b was also identical to Experiment 5, except that the order of arenas was reversed, thus, counterbalancing the order of presentation of arenas. For clarity, during stage 1 of Experiment 6b, participants completed 24 trials in the trapezium-shaped arena which contained four red landmarks and, in stage 2, participants completed 24 trials in the kite-shaped arena which contained four blue landmarks (see Figure 3.5). Only details pertaining to the shape recognition task are reported in the following section.

3.3.1.1 Participants

For Experiment 6a, 48 participants were recruited from the University of Nottingham (24 male), aged between 18 to 47 years (mean = 22.79, *SD* = 4.92). Participants were allocated to each of the four groups in pseudo-random manner to ensure an equal number of males (6) and females (6) were present in each group. For Experiment 6b, a further 48 participants (20 male) were also recruited from the University of Nottingham. The age of participants ranged from 18 to 30 years (mean = 20.52, *SD* = 2.34), and they were again pseudo-randomly allocated to each group to ensure there were the same number of males (5) and females (7) in each group. For both experiments, participants were given course credit or £5 in return for participation, and an additional £10 was awarded to the participant who completed each experiment in the shortest time.

3.3.1.2 Materials

Black lined and white filled pictures of a kite (on screen wall lengths of 35mm and 108mm) and trapezium (on screen wall lengths of 35mm, 108mm, and 69mm) were created using Microsoft PowerPoint 2007. Pictures of an isosceles triangle (on screen wall lengths of 108mm and 60mm) and a regular parallelogram (on screen wall lengths of 86mm and 60mm), were also created as distracter stimuli. All stimuli were presented on a white background. This task was run on a standard sized (476.6 mm x 268.1 mm) computer monitor. Experimental events were controlled and responses recorded by PsychoPy (Peirce, 2007; www.psychopy.org).

3.3.1.3 Procedure

Following the ID-ED task, the shape recognition task was administered, during which participants were then sat not more than 50 cm in front of a standard sized computer monitor and presented with the following, on screen instructions:

For the final stage of the experiment you will be presented with pictures of different shapes. It is your task to decide which of these shapes match the shapes of the arenas that you previously navigated.

Please press "Y" if you think you were in the shape before.

Please press "N" if not.

Take as much time as you need to make your decision.

On each trial, a kite, trapezium, triangle or parallelogram, was presented in the centre of the computer monitor. Each picture was presented in two different orientations during the task. The kite and triangle were each presented once with their most acute corner facing the left side of the computer monitor, and once with their most acute corner facing the right side of the computer monitor. The trapezium was presented once with its smallest side facing the top of the monitor, and once with its smallest side facing the bottom of the monitor. On both trials, the parallelogram was presented with its two longest sides running parallel to the top of the monitor. On one trial, the two acute corners were to the top right and bottom left of the shape, on the other trial the two acute corners were to the top left and bottom right of the shape (see Figure 3.8). The order of presentation of the 8 stimuli was randomised independently for each participant. Below each picture, centred, were the following on screen instructions:

Were you in this shape? (Y/N)

Trials were self-paced, with each trial terminating when the participant pressed either the “Y” or “N” key. The subsequent trial began immediately after the termination of the preceding trial. After all 8 trials, the screen was cleared and participants received on screen instructions to contact the experimenter.

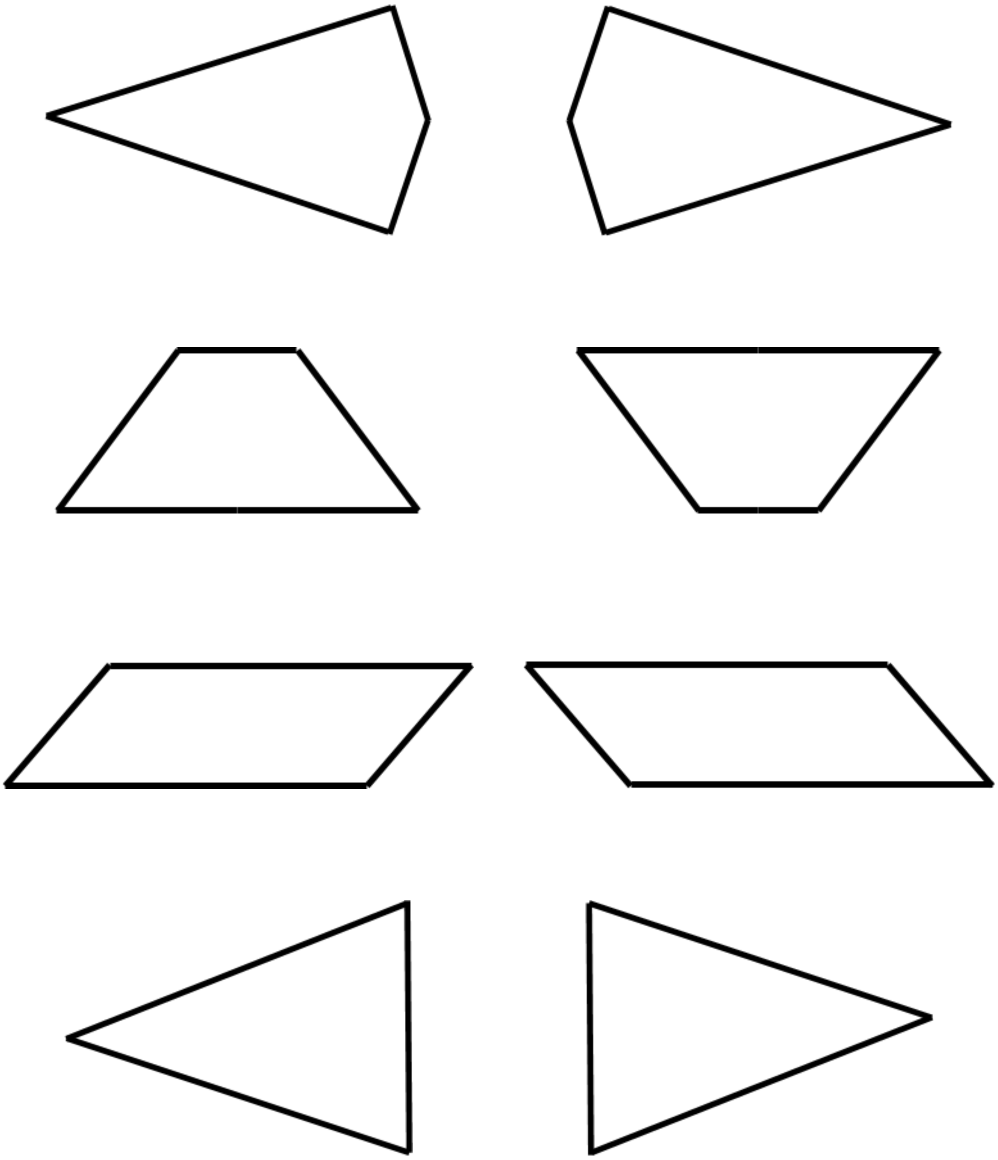


Figure 3.8. Pictures of the 8 stimuli that were used in the shape recognition task of Experiment 6, shown in the orientation in which they were presented to participants.

3.3.2 Results

As Experiments 6a and 6b were two halves of a counterbalanced procedure, data from the two experiments were collapsed together in both the analysis of navigational behaviour, and in the analysis of the shape recognition task.

3.3.2.1 Intradimensional-Extradimensional shift

Stage 1. Figure 3.9 shows the latency to find the hidden goal, in seconds, during the 24 trials of stage 1 in the four groups. All groups showed a reduction in the latency to find the goal as trials progressed, although it appeared that the groups for which landmarks were relevant may have found the goal quicker early in training. A two-way ANOVA of individual latencies to find the goal, with a between-subjects variable of relevant cue in stage one (landmarks or shape), and a within-subjects variable of trial (1-24), revealed significant main effects of relevant cue $F(1, 94) = 4.37$, $MSE = 521.67$, $p = .039$, $\eta_p^2 = .04$, trial $F(23, 2162) = 96.82$, $MSE = 95.33$, $p < .001$, $\eta_p^2 = .51$, and a significant interaction between relevant cue and trial $F(23, 2162) = 4.80$, $MSE = 95.33$, $p < .001$, $\eta_p^2 = .05$. Simple main effects analysis revealed that groups for which landmarks were relevant were quicker to find the goal on trials 1 and 4 only Fs$(1, 94) > 9.75$, MSEs < 931.28, ps$= .002$, $\eta_p^2 > .09$.

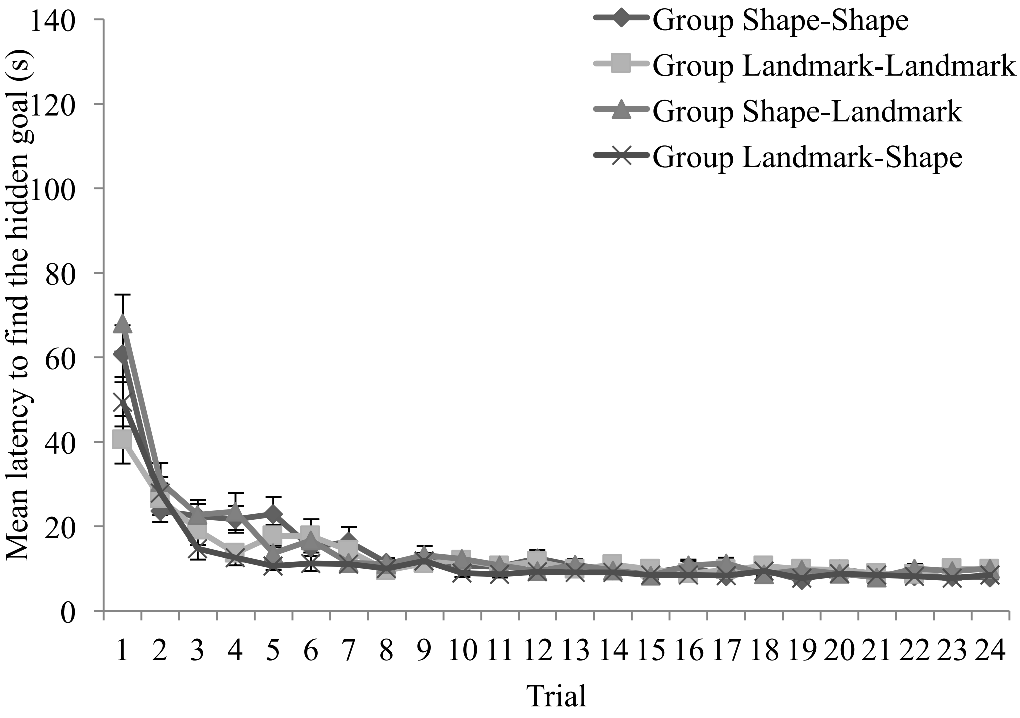
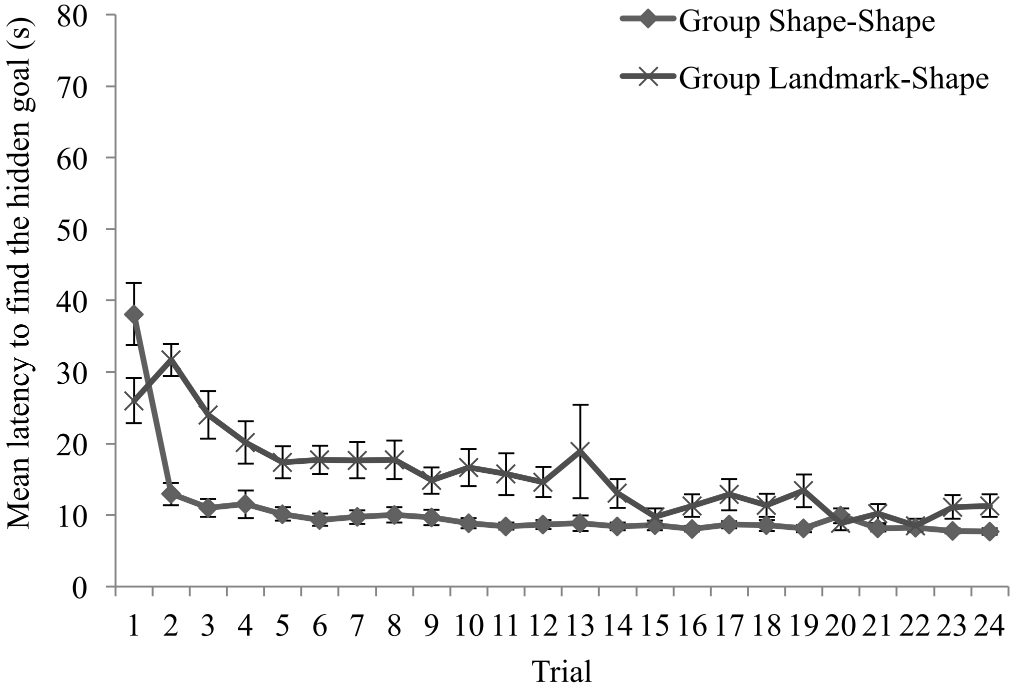


Figure 3.9. Mean latencies of the four groups to find the hidden goal in stage 1 of Experiment 6. Error bars show 1 +/- standard error of the mean.

Stage 2. The mean latencies to find the goal during stage 2 are shown in the top panel of Figure 3.10 for groups shape-shape and landmark-shape, and in the bottom panel of Figure 3.10 for groups landmark-landmark and shape-landmark. In keeping with the results of Experiments 4 and 5, both groups that performed an ED shift (groups landmark-shape and shape-landmark) showed longer latencies to find the goal relative to the appropriate ID groups (groups shape-shape and landmark-landmark, respectively). A three-way ANOVA of individual latencies to find the goal, with the between-subjects variables of shift (ID or ED) and relevant cue in stage 2 (shape or landmarks), and the within-subjects variable of trial (1-24), revealed significant main effects of shift *F*(1, 92) = 57.00, *MSE* = 580.17, $p < .001$, $\eta_p^2 = .38$, trial *F*(23, 2116) = 23.61, *MSE* = 85.62, $p < .001$, $\eta_p^2 = .20$, but not



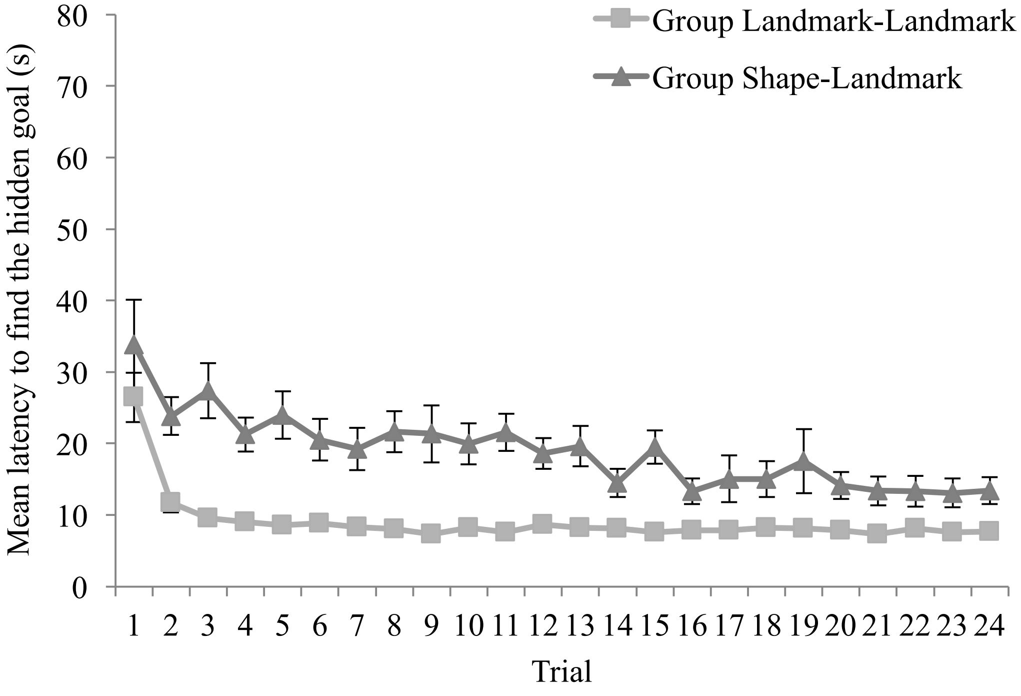


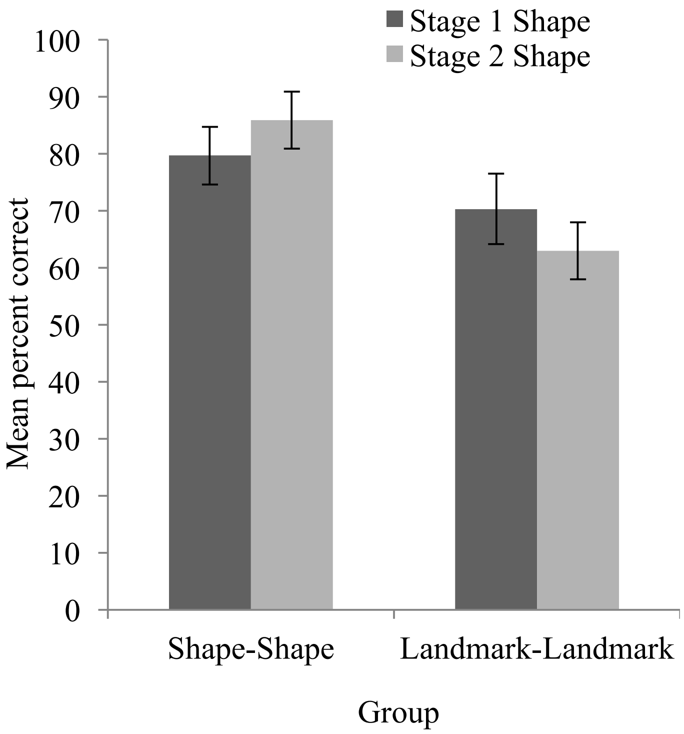
Figure 3.10. Top: Mean latencies of groups shape-shape and landmark-shape to find the hidden goal in stage 2 of Experiment 6. Bottom: mean latencies of groups shape-landmark and landmark-landmark to find the hidden goal in stage 2 of Experiment 6. Error bars show 1 +/- standard error of the mean.

relevant cue $F<1$. Importantly, the interaction between shift and trial was significant $F(23, 2116) = 4.83$, $MSE = 85.62$, $p< .001$, $\eta_p^2 = .05$. Simple main effects analysis of this interaction revealed that whilst there was no difference between the ID and ED groups on trial 1 $F<1$, the ED groups were significantly slower to find the goal on trials 2-24 Fs(1, 92) > 4.81, MSEs < 311.26, ps< .031, $\eta_p^2 > .05$. The two-way interaction between relevant cue and trial was not significant $F<1$, but the interaction between relevant cue and shift was significant $F(1, 92) = 5.50$, $MSE = 580.17$, $p= .021$, $\eta_p^2 = .06$. Simple main effects analyses revealed that, for both landmark and shape relevance, the ED groups were significantly slower to find the goal in stage 2, overall, than the ID groups Fs(1, 92) > 13.55, MSEs = 24.17, ps< .001, $\eta_p^2 = .13$. There was no difference in the time taken to find the goal during stage 2 in the ID groups, $F<1$, although, in the ED groups, the landmark-shape group were quicker to find the goal in stage 2 compared to the shape-landmark group $F(1, 92) = 5.54$, $MSE = 24.17$, $p= .021$, $\eta_p^2 = .06$. Finally, the three-way interaction between shift, relevant cue, and trial was not significant $F(23, 2116) = 1.45$, $MSE = 85.617$, $p= .076$, $\eta_p^2 = .02$.

3.3.2.2 Recognition task

During the recognition test, it is possible that the two distractor stimuli (parallelogram and triangle) both acted as foils for each of the two target stimuli (kite and trapezium). Consequently, the total number of “Yes” responses to the kite target pictures and “No” responses to the triangle and parallelogram distracter pictures were summed, and divided by the total number of responses made to these pictures to calculate a percent correct score for the kite arena. Similarly, the total number of "Yes" responses to the trapezium target pictures and "No" responses to the triangle and parallelogram distracter pictures were summed, and dividing this number across the total number of responses made to these pictures to calculate a percent correct score for the trapezium arena.

Figure 3.11 shows the mean percent correct recognition for the shapes navigated in stage 1 and stage 2, for each of the four groups in the experiment. First, and consistent with the notion that navigation permitted the extraction of global representations of the shapes of the arenas, recognition of the stage 1 and stage 2 target shapes appeared above chance in all four groups. It appeared, though, that while both ED groups displayed equivalent performance, group shape-shape had higher recognition scores than group landmark-landmark. First, one sample t-tests were conducted to assess if individual recognition scores for the navigated shape in stage 1 and stage 2 of the experiment were above chance. In the shape recognition task, four out of the eight presented shapes matched the navigated arenas, giving a chance level of 50%. However, in the calculations previously described, a maximum of two correct "Yes" responses to target shapes were summed with four responses made to the distracter pictures, giving a chance level of 33.33%. Taking the conservative value of a 50% chance level, recognition of the navigated shapes in both stage 1 and stage 2 were above chance in all four groups $ts(23) > 3.33$, $p<.003$.



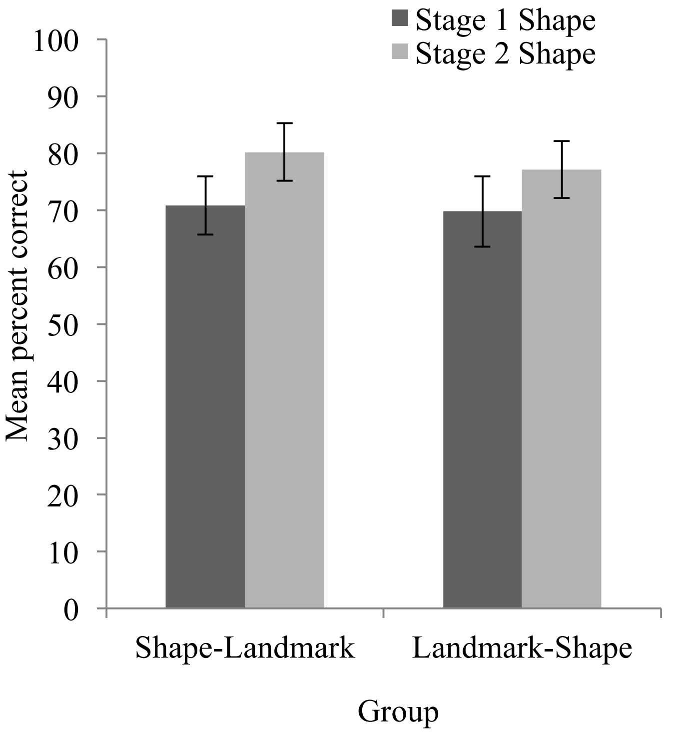


Figure 3.11. Mean percent correct recognition of the shapes navigated during stage 1 and stage 2 in the intradimensional (top) and extradimensional (bottom) groups of Experiment 6. Error bars show +/- 1 standard error of the mean.

Second, individual percent correct scores were treated with a three-way ANOVA, with between-subjects variables of shift (ID or ED) and relevant cue in stage one (shape or landmarks), and a within-subjects variable arena (stage 1 or stage 2). This revealed no significant effects of shift $F<1$, or arena $F(1, 92) = 1.20$, $MSE < 756.41$, $p=.277$, $\eta_p^2 = .01$, although there was a simple main effect of relevant cue $F(1, 92) = 4.98$, $MSE = 756.41$, $p=.028$, $\eta_p^2 = .05$. There was, however, a significant interaction between shift and relevant cue $F(1, 92) = 4.98$, $MSE = 756.41$, $p=.028$, $\eta_p^2 = .05$. Simple main effects analysis of this interaction revealed a significant difference between the shape-shape and landmark-landmark groups $F(1, 92) = 9.95$, $MSE = 378.20$, $p=.002$, $\eta_p^2 = .10$: participants in the shape-shape group displayed significantly better recognition of the navigated shapes compared to participants in the landmark-landmark group. There were no differences in shape recognition between the shape-shape and landmark-shape group, the landmark-landmark and shape-landmark group, or the shape-landmark and landmark-shape groups $Fs(1, 92) < 2.57$, $MSEs = 378.20$, $ps > .11$, $\eta_p^2 > .03$. Returning to the results of the ANOVA, the interactions between shift and arena $F(1, 92) = 1.54$, $MSE = 271.80$, $p= .218$, $\eta_p^2 = .02$, relevant cue and arena $F(1, 92) = 1.20$, $MSE = 271.80$, $p=.277$, $\eta_p^2 = .01$, and the three-way interaction $F<1$, were not significant.

3.3.3 Discussion

In keeping with the results of Experiment 5, navigating on the basis of stimuli drawn from one dimension retarded subsequent navigation if the relevant stimuli were drawn from a different dimension. To reiterate a point made earlier, the retardation of group landmark-shape relative to group shape-shape is not predicted by theories that state boundary information is processed in a fashion immune to interference from learning about landmarks (e.g. Cheng, 1986; Doeller & Burgess, 2008; Gallistel, 1990), or by the theory proposed by Miller and Shettleworth (2007, 2008, 2013).

Experiment 6 is particularly novel in its use of the final shape recognition test to assess participant's global representation of the arenas navigated. Importantly, and contrary to theories that suggest this knowledge is acquired independently of the presence of the other cues, knowledge about the global structure of the shape of the environments was modulated by varying the relevance of the shape and/or the landmarks. The shape-shape group displayed good recognition of the target stimuli following training in which the shape of the arena was relevant to finding the goal throughout the experiment. Training in which the shape of the arena was irrelevant for finding the goal throughout the experiment limited the extent to which the global structure of the boundaries was encoded and, ultimately, rendered it less recognisable at test for the landmark-landmark group. Clearly then, acquisition of knowledge about the global-shape of an environment is affected by the presence of other, non-boundary, cues. It is, perhaps, not surprising that the recognition scores did not differ between the two ED groups because, for one half of the experiment, the boundary shapes of the arena were relevant to finding the goal whereas, for the remainder of the experiment, the landmarks were relevant.

3.4 General Discussion

In four experiments, participants were required to find a hidden goal in a virtual arena that contained distinctive landmarks. Either the shape of the arena, or the location of the landmarks, was made relevant to navigating towards the hidden goal. In each experiment, participants were faster to find the goal when the dimension relevant to finding the goal was the same as during previous sessions of navigation. These results were obtained when the landmarks were spatially integrated into the boundary of the arena (Experiment 4), or when they were spatially separated from the boundary as intra-arena cues (Experiments 5 and 6a and 6b). Experiments 6a and 6b revealed that participants' ability to recognise the shape of the arenas that they had previously navigated was influenced by whether shape had been established as relevant to finding the goal during the first stage of the experiment.

As noted earlier, these results are difficult to reconcile with theories of spatial learning that place an emphasis on the special status of the shape of an arena in navigation. According to a number of theories (e.g. Cheng, 1986; Gallistel, 1990) learning about the shape of an arena involves the acquisition of a global representation of the geometric relations of the arena that is impervious to interference from learning about landmark information. The results of Experiments 6a and 6b are, in particular, relevant to this suggestion. Participant's recognition of the shape of the arenas was significantly greater than chance, a result compatible with forming of representation of the global-shape of the arenas. However, recognition of the navigated arenas in the experiment was impaired if landmarks were relevant throughout the duration of the experiment, relative to if shape was relevant throughout the experiment. Previous studies of the interaction of landmarks and shape cues in studies of either human or animal spatial learning have not reported any measure of participants' knowledge of the global-shape of the arena previously navigated (e.g. Doeller & Burgess, 2008; Pearce et al., 2006; Redhead & Hamilton, 2009). The current results, therefore, seem to constitute the first demonstration of an interference of the global representation of the shape of an arena by navigation with local landmarks.

The results of the current experiments permit further constraints to be placed upon explanations of spatial navigation that have, as their basis, associative theories of learning. The ID-ED effects noted in the four experiments reported in this chapter are inconsistent with the proposals of Miller and Shettleworth (2007, 2008, 2013). Their model assumes that the salience of stimuli (α) is fixed, and for an associative model to be capable of explaining ID-ED effects, changes in the attention paid to relevant and/or irrelevant dimensions must be permitted. For example, according to Mackintosh (1975), the change in the associative strength of a target cue (ΔVT) progresses according to Equation 3:

$$\Delta VT = \alpha T\ (\lambda - VT) \qquad \text{Equation 3.}$$

Here, αT is the attention paid to the target cue, β is a learning rate parameter determined by the properties of the outcome, and λ is the asymptote of learning supported by the outcome. Crucially, according to Mackintosh (1975), the attention paid (α) to a cue increases if it is a better predictor of the outcome than all other cues present on a trial, and decreases if it is no better a predictor of the outcome than all the other cues present on a trial. The rules specified by Mackintosh for determining these increases and decreases to a target cue (T) are shown in Equations 4a and 4b:

$$\Delta\alpha T > 0 \text{ if } |\lambda - VT| < |\lambda - Vr| \qquad \text{Equation 4a.}$$

$$\Delta\alpha T < 0 \text{ if } |\lambda - VT| \geq |\lambda - Vr| \qquad \text{Equation 4b.}$$

Here, Vr is the sum of the associative strength of all available cues, minus VT (that is to say, the remainder). The size of the change in α is assumed to be proportional to the magnitude of the inequalities in Equation 4a and 4b. Thus, cues which are good predictors of subsequent events will gain an increase in their salience – or attention. Irrelevant cues that are poor predictors of subsequent events, however, suffer a reduction in their attention (see also: Esber & Haselgrove, 2011; Le Pelley, 2004). In order to explain instances of the ID-ED effect, Mackintosh proposed that attention generalizes among stimuli in proportion to their similarity (p. 292). Consequently, attention should generalize more between cues that are drawn from the same dimension (such as the common features of two different environmental shapes, or two different sets of landmarks) than between cues that are drawn from different dimensions. On the basis of these two proposals, it is relatively straightforward to understand why learning, in stage 2, was slower in the two ED groups than the two ID groups. Training in stage 1 in groups landmark-landmark and landmark-shape should ensure that, by the end of this stage, attention will be higher to the relevant landmarks within the arena than its irrelevant shape. In contrast, stage 1 training in groups shape-shape and shape-landmark should ensure that attention is higher to the relevant shape of the arena, than the landmarks within it. This training should benefit stage 2 learning in groups landmark-landmark and shape-shape, as the high attention paid to the relevant cues in stage 1 of the training, will generalize to the cues that continue to be relevant in stage 2. However, the same will not be true for groups landmark-shape and shape-landmark. For these two groups, the high attention acquired to the relevant cues in stage 1 will generalize to cues that are subsequently irrelevant to learning in stage 2, hindering performance in the task.

It is appropriate to consider, at this juncture, the relevance of the current experiments to other studies that have investigated the effects of stimulus relevance on learning, both in general, and more specifically in the domain of spatial learning. The results of many studies are now converging upon the conclusion that establishing a set of cues as relevant to acquiring a goal, or trial outcome, results in these cues acquiring more attention than the cues from another set that are irrelevant to acquiring the goal (for a review see: Le Pelley, 2010). As seen in the current experiments, as well as other demonstrations of the ID-ED effect (e.g. George & Pearce, 1999; Mackintosh & Little, 1969; Roberts, Robbins, & Everitt, 1988), learning about cues is faster when they have been established as relevant, rather than irrelevant, predictors of goals – a result that is consistent with the idea that these cues are attracting more attention and are, thus, more associable (see also: Le Pelley & McLaren, 2003). Furthermore, experiments have shown that relevant cues are less prone to the attentional blink than are irrelevant cues (Livesey, Harris, & Harris, 2009); support a dot probe effect (Le Pelley, Vadillo, & Luque, 2013), and attract more eye gazes (Le Pelley, Beesley, & Griffiths, 2011) than irrelevant cues. Studies of the influence of relevance training on stimulus attention are widespread in non-spatial literature, and the experiments presented in this chapter, alongside previous spatial learning experiments (Cuell et al., 2012; Trobalon et al., 2003), suggest similar associative mechanisms govern learning in both spatial and non-spatial domains. The results of the experiments presented in this chapter, therefore, join a more general class of studies demonstrating the role of stimulus relevance on associability and attention in spatial learning. Where they distinguish themselves, of course, is with the more specific conclusions that can be drawn about the influence of relevance training on the representation of the shape of the arena being navigated. Given that relevant cues have been shown to attract more eye gazes than irrelevant cues in studies of predictive learning in humans (Le Pelley et al., 2011), it would be interesting to assess if shape or landmark relevance training alters the overt attention paid to these cue dimensions. Eye-tracking procedures, in which sampling times and distributions of visual foci are recorded, have been utilised in virtual navigation procedures previously (e.g. Mueller, Jackson, & Skelton, 2008; Hamilton, Johnson, Redhead, & Verney, 2009), and would offer a potential approach to address this issue.

Although modular theories of geometric information processing continue to be a matter of theoretical influence (e.g. Gallistel & Matzel, 2013; Spelke & Lee, 2012; Jeffrey, 2010), it is relevant to note that Cheng has recently explored how a view-based navigational theory might succeed in explaining spatial navigation (Stürzl et al., 2008; See also: Cheng, 2005, 2008; Cheng & Newcombe, 2005). This theory uses a mathematical function to determine the difference between the current global image and stored global images of nearby locations. Gradient descent is then used to model the movement of the organism away from the current position, and towards locations successively closer to the goal. Although this theory has had some success in explaining how learning in an environment of one shape can transfer to an environment of another shape (Cheung et al., 2008), the results of the current experiments may prove to challenge it, as the theory uses veridical images to represent the environmental stimuli, unadjusted for variations in attention. The theory proposed by Stürzl et al., therefore, seems to encounter the same problem when attempting to explain the basic ID-ED effect as Miller & Shettleworth's (2007, 2008, 2013) model.

One problem that any theory of spatial navigation, associative or otherwise, has to address is how participants are able to correctly identify, from a novel perspective, the arena that had previously been navigated. Similar view-independent recognition effects have been reported elsewhere (e.g. Christou & Bulthoff, 1999; Hock & Schmelzkopf, 1980), but it must be acknowledged that, in the field of object recognition, demonstrations of complete viewpoint invariance are difficult to obtain (Farah, Rochlin, & Klein, 1994; Rock, Wheeler, & Tudor, 1989). Biederman (1987) suggested that an object (and by generalization, a view) could be recognised from a different perspective so long as the similarity between the views is sufficiently high, and so long as the relationship between the components of the views were not altered. Although the similarity of the components used during the navigation and recognition tests of Experiments 6a and 6b was particularly low, it is conceivable that recognition was achieved by matching the relationships between the components of the scenes. For example, during navigation within the kite-shaped arena, participants will encounter particular structural conjunctions of wall lengths (long-short, short-short, short-long and long-long) – the same conjunctions that are present in the plan view of this arena. Although it remains to be determined exactly how such conjunctions could be matched when the components upon which they are based are so different, the encoding of such structural information has been investigated and modelled from the perspective of associative learning (George, Ward-Robinson, & Pearce, 2001; Haselgrove, George, & Pearce, 2005).

3.4.1 Conclusion

The results of the four ID-ED experiments reported here demonstrate that establishing the boundary shape of an environment as irrelevant to finding a hidden goal in a virtual environment retards subsequent learning about a novel boundary shape, relative to a group in which the boundary shape of the environment was never irrelevant. The same findings were also observed with landmark cues. These results are not consistent with the notion that learning to environmental boundaries occurs incidentally (e.g. Doeller & Buress, 2008), or theories which suggest that the salience of cues is not modifiable (e.g. Miller & Shettleworth, 2007, 2008, 2013). By permitting changes in attention and, thus, what is learned about relevant and irrelevant cues (e.g. Esber & Haselgrove, 2011; Le Pelley, 2004; Mackintosh, 1975), associative analyses of spatial learning will provide an explanation of these results.

Chapter 4

Learned predictiveness training modulates biases towards using boundary or landmark cues during navigation

In Chapter 1, it was noted that a number of experiments have failed to find evidence of landmarks overshadowing learning about the boundary shape of an environment (e.g. Doeller et al., 2008; Hayward et al., 2004; Hayward et al., 2003; Graham et al., 2006; McGregor et al., 2009; Redhead & Hamilton, 2007; Wall et al., 2004) For instance, Doeller and Burgess (2008) conducted an experiment in which participants were required to collect a number of objects within a virtual environment and, having collected the objects, were asked to replace a given object. Distance errors between where the object was replaced and its original position provided a measure of performance. Participants in a compound group were trained in a circular arena that was orientated by distal cues, and that contained an intramaze landmark. Following acquisition, participants in the compound group were given one of two test phases. For one half of the participants the circular boundary was removed, such that the objects had to be replaced by reference to just the landmark cue whereas, for the other half of the participants, the landmark cue was removed, such that the objects had to be replaced with reference to just the circular boundary. Performance was compared to two control groups that performed the whole experiment with only the landmark or the circular boundary, as well as the orientation cues. While participants in the compound group who were tested with the circular boundary showed equivalent performance to the boundary control group, participants in the compound group who were tested with the landmark cue displayed greater error compared to the landmark control group. Consequently, the circular boundary cue was said to have overshadowed learning about the intramaze landmark, but learning about the circular boundary was immune to overshadowing. As already noted, the apparent inability of landmark cues to overshadow learning about information provided by the boundary shape of an environment has led a number of authors to conclude that boundary information holds a special status when learning to navigate, such that this learning is impervious to the influence of landmark cues (Doeller & Burgess, 2008; see also Cheng, 1986; Gallistel, 1990; Wang & Spelke, 2002, 2003).

There are, however, a number of problems with using the observation that a landmark is unable to overshadow learning about information provided by boundary walls to conclude that boundary information holds a special, impervious, status when learning to navigate. First, a failure to observe overshadowing may be accounted for with a mechanism that is incorporated into associative theories of learning, namely, generalisation decrement (e.g. Pearce, 1987). Consider the compound group in the experiment conducted by Doeller and Burgess (2008), in which the small landmark cue was removed for one half of participants during the test trials. This, potentially, minor change from the conditions of training would lead to the training and test environments appearing visually similar and, thus, performance may not deteriorate relative to the control group trained with only the boundary wall. In contrast, for the other half of the participants in the compound group, the large circular boundary was removed at test. This more substantial change from the conditions of training could be expected to lead to the training and testing environments appearing visually different. There would, therefore, be a large deterioration in performance in these participants that would give the impression of an overshadowing effect relative to the control group only trained with a landmark cue. Second, as already reviewed, there are now a number of published demonstrations of a landmark cue successfully overshadowing learning about shape information provided by the boundaries of an arena (Cole et al., 2011; Horne et al., 2010; Horne & Pearce, 2011; Pearce et al., 2006).

Any theory which states that information provided by the boundary walls of an environment is learned about independently from landmark cues (e.g. Cheng, 1986; Gallistel, 1990), or in a manner inconsistent with theories of associative learning (e.g. Doeller & Burgess, 2008), struggles to explain instances where landmarks have successfully overshadowed learning about information provided by the boundaries of an environment. There is, however, a need to address why overshadowing experiments conducted within the spatial domain, which have essentially followed the same protocol, produce contradictory findings – especially given that modular theories of geometric and boundary information processing continue to be a matter of theoretical influence (e.g. Doeller & Burgess, 2008; Gallistel & Matzel, 2013; Jeffrey, 2010; Spelke & Lee, 2012). In studies of non-spatial learning, the relative salience of two cues presented in compound has been shown to impact upon which cue will take control of behaviour. For example, Mackintosh (1976) trained rats that a compound of a light and a noise signalled an impending shock, and compared learning to control groups trained with either the light or noise in isolation. Throughout the experiment, the intensity of the light was kept constant, but the intensity of the noise was manipulated. In the compound group, a noise of 85dB overshadowed learning to the light when compared to learning in the light control group. In contrast, the light overshadowed learning about 60dB or 50dB noises compared to leaning in noise control groups trained with 60dB or 50dB noises, respectively (see also Miles & Jenkins, 1973).

The experiments reported in Chapter 3 demonstrated that establishing either landmarks, or the geometry of the environment, as relevant to navigation influenced the speed at which novel stimuli drawn from these stimulus dimensions were subsequently learned about. Participants were slower to find a hidden goal when the novel cues were from a dimension that had previously been irrelevant, rather than relevant, for navigation. As noted in the general discussion of Chapter 3, in order to account for these results, it is necessary for models of spatial learning to permit changes in the attention paid to relevant and irrelevant stimuli in a manner envisaged by attentional models of learning (e.g. Esber & Haselgrove, 2011; Le Pelley, 2004; Mackintosh, 1975). In addition to providing an explanation for the ID-ED effects observed in Chapter 3, attentional models of learning also offer a possible explanation for why, in some circumstances, landmarks overshadow learning about boundary shape but, in other circumstances, fail to overshadow learning about boundary shape. According to Mackintosh's theory, for example, cues which enter an experiment with inherently high salience will gain attention if they are learned about in compound with a cue that is of a lower inherent salience (which itself will suffer a loss in attention). This process will permit the cue that is more salient to overshadow the less salient cue, but not vice versa.

The impact of the relative salience of landmark and boundary cues in determining which cue takes control of behaviour has largely been ignored in the spatial learning literature. There seems to be only one other study that has directly examined the relative salience of landmark and boundary cues in cue competition experiments, which will be discussed in the general discussion. This omission is relatively surprising given the theoretical (e.g. Mackintosh, 1975), and empirical (Mackintosh, 1976; Miles and Jenkins, 1973), impact that cue salience has on overshadowing. One reason for this oversight, perhaps, is the difficulty in manipulating the unconditional salience of landmark and boundary cues. While it is intuitive to assume that louder noises are more salient than quieter noises and, thus, when presented in compound with a light to expect that there will be a level of noise intensity at which learning to the light will be overshadowed, it is not clear how to manipulate the unconditional salience of landmark or geometry cues in a similar manner. It might be expected that increasing the size of a landmark would increase its salience, but it is possible to imagine a landmark so large that it would not be an effective cue by which to localise a goal location. Manipulating the wall length ratio of, say, a kite might be a way in which to alter the unconditional salience of a particular corner, but it is possible to imagine a situation where the obtuse corner is almost imperceptible. Even if there were reliable ways of manipulating the salience of landmarks and boundaries, it is not practical, on a participant by participant basis, to judge the relative salience of the two cues *a priori* and, thus, predict which cue may take control of behaviour. Considering this, it is not unreasonable to suggest that spatial overshadowing experiments might be confounded by the relative salience of the boundary and landmark cues. If experimenters used boundary cues that were relatively more salient than landmark cues, then it is likely that the landmarks would have failed to overshadow learning about the boundary, a result that, at face value, would be consistent with modular processing of boundary wall information. If, however, experimenters used boundary cues that were relatively less salient than landmark cues, it is likely that the landmarks would have successfully overshadowed learning about boundaries, a result apparently more consistent with an associative analysis of spatial navigation.

The experiments reported in this chapter were designed to examine if the relative salience of landmark and boundary cues could account for why, in some circumstances, landmarks fail to overshadow learning about the boundary walls of an environment and, in other circumstances, successfully overshadow learning about boundary walls. Given the foregoing discussion relating to the difficulty in manipulating the relative unconditional salience of landmark and boundary shape information, salience was manipulated more centrally by driving attention towards a particular cue dimension prior to compound training by using a learned-predictiveness procedure. Studies conducted in the spatial domain with human (Chapter 3) and non-human (Cuell et al., 2012) animals have shown that establishing one spatial cue as predictive of a hidden goal location, and another cue as irrelevant, facilitates subsequent learning about the predictive cue in a manner that is consistent with attentional analyses of learning (e.g. Esber & Haselgrove, 2011; Le Pelley, 2004; Mackintosh, 1975). Experiment 7 sought to exploit these observations in order to investigate whether establishing either landmarks or shape information provided by the boundary walls of an environment as relevant to navigation would influence the dominance of these cues when they were subsequently established as equally predictive of a hidden goal during subsequent compound training (see Duffaud, Killcross, & George, 2007).

Recall that in an overshadowing design, participants are trained with a compound cue (AB) before receiving a test trial with only, say, cue A. The removal of one cue from the compound can result in a reduction in performance at test simply because of the change in conditions between training and testing (i.e. generalisation decrement). It is, therefore, difficult to determine whether any attenuated performance at test is due to overshadowing or generalisation decrement. Given that it has been noted that the data from previous overshadowing experiments conducted in the spatial domain might be explained via generalisation decrement (e.g. Doeller & Burgess, 2008), the current experiment did not attempt to assess cue salience through a traditional overshadowing test. Instead, at test, both landmark and boundary information were presented, but the two sources of information were placed into spatial conflict with each other (see methods, Experiment 7). Unlike the overshadowing experiments discussed earlier, as both landmark and boundary cues are presented during the conflict tests, any preference towards one particular cue domain cannot be explained via generalisation decrement. Assessing cue salience via conflict tests also has the additional benefit of being particularly sensitive. When landmark and shape cues, that were previously trained in compound, are presented in isolation, it is possible that participants will search by each cue for a similar amount of time as there is simply no other behaviour to perform during the test. When both cues are presented during the same test, however, participants are given the opportunity to search near both cues. Any slight difference in salience between the cues, which may not be detected when presenting each cue in isolation, would be expected to translate into a preference for searching near one cue over another during a conflict test.

4.1 Experiment 7

Stage 1 of Experiment 7 was equivalent to stage 1 of Experiment 5. Consequently, participants were required to find a hidden goal that was located in one of the corners of a virtual kite-shaped arena that contained a differently shaded blue sphere in each corner. On every trial, these blue spheres changed position. For a landmark-relevant group, the hidden goal was located by the same sphere on each trial during stage 1. Consistent with the landmark-landmark group of Experiment 5, therefore, to find the goal participants would have to approach the same landmark regardless of which corner that landmark was in. For a shape-relevant group, the hidden goal was located in the same corner of the kite during each trial of stage 1. Consistent with the shape-shape group of Experiment 5, in order to find the goal, participants would have to approach the same corner regardless of which landmark was present at that corner. The experiments described in Chapter 3 have confirmed that this training alters the salience of the landmarks and boundaries of the arena in a manner consistent with attentional models of learning (e.g. Esber & Haselgrove, 2011; Mackintosh, 1975). Thus, for the landmark-relevant group, landmarks will be more salient than the arena boundaries, and vice versa for the shape-relevant group. Following training in the kite, both groups proceeded to stage 2, during which participants were trained to find a hidden goal in a trapezium-shaped arena that contained a differently-shaded red landmark in each corner. The landmarks remained in the same corner throughout each trial, thus, in order to find the hidden goal participants could rely on: (1) information provided by the landmarks within the arena, (2) information provided by the shape of the arena itself, or (3) a combination of both the landmark and shape cues. To establish which cue dimension, if any, was dominating behaviour, three test trials were intermixed within stage 2 training trials. During each test trial, in which the hidden goal was not present, the landmark and shape cues were placed in conflict with each other by rotating the configuration of landmarks relative to the boundary shape.

For participants given landmark-relevance training in stage 1, landmark cues were expected to be relatively more salient than the shape information provided by the boundary walls at the onset of stage 2 training. The landmark cue should, therefore, be the more dominant cue during compound training and, thus, participants would search for longer near the landmark cue during the conflict test relative to the appropriate corner of the shape. In contrast, for those given shape-relevance training in stage 1, the shape information provided by the boundary walls should be relatively more salient than the landmark cues at the onset of stage 2 training. The shape information provided by the boundary walls should, therefore, be the more dominant cue during compound training and, thus, participants should search for longer near the appropriate corner of the arena during the conflict tests, compared to near the appropriate landmark cue.

4.1.1 Method

4.1.1.1 Participants

24 participants were recruited from the University of Nottingham (18 female). Participants were allocated randomly to either the shape-relevant or landmark-relevant group, with the constraint that the genders were balanced between the two groups. Participants were given course credit or £5 in return for participation. The age of participants ranged from 18 to 27 years (mean = 20.83, *SD* = 2.60). An additional £10 was awarded to the participant who completed stage two of the experiment in the shortest time.

4.1.1.2 Materials

As with the previous experiments reported in this thesis, all virtual environments were constructed and displayed using Mazesuite software (Ayaz et al., 2008; www.mazesuite.com), and were run on the same computer and screen reported in Experiment 1. The dimensions of both the kite- and trapezium-shaped environment, and the colour of the walls used to construct the arenas, were identical to those used in Experiments 4-6. The four distinctly coloured blue spheres that acted as landmarks within the kite-shaped arena, and the four distinctly coloured red spheres acted as landmarks within the trapezium-shaped arena, were identical to those reported in Experiment 5 and 6 (see Figure 3.5). Also in keeping with Experiment 5 and 6, all landmarks were 90cm in diameter, and were located 1.48m away from the apex of each corner, on a notional line that bisected the corner. As with the experiments reported in Chapter 2 and 3, the goals within the kite- and trapezium-shaped arenas were square-shaped regions (1.08m x 1.08m) that were located 1.48m away from the walls of the arena, along on a notional line that bisected the corner. Finally, the same exploration arena that was reported in Experiment 1 was, again, used to allow participants to become familiar with the controls of the experimental task.

4.1.1.3 Procedure

After signing a standard consent form, participants were given the following set of instructions on paper:

This study is assessing human navigation using a computer generated virtual environment. During this experiment, you will complete 43 trials. In each trial, you will be placed into a room that contains an invisible column. Your aim is to end the trials as quickly as possible by walking into the column.

You will view the environment from a first person perspective, and be able to walk into the column from any direction using the cursor keys on the keyboard. Once you've found the column a congratulatory message will be displayed and you should hit enter when you're ready to begin the next trial. You will always be in the centre of the arena when a trial begins, but the direction in which you face at the start of each trial will change.

To start with, you may find the column is difficult to find. There is, however, a way of learning exactly where the invisible column will be on each trial. It's a good idea to fully explore the environment on the first few trials; this will help you to learn where the column is going to be.

This session should take around 15 minutes. If at any point you wish to stop this session, please notify the experimenter and you'll be free to leave without having to give a reason why. Your results will be saved under an anonymous code, and kept confidential throughout.

The person who takes the least time to complete this experiment will win a £10 prize!

In keeping with the experiments reported in previous chapters, participants sat not more than 100 cm from the screen, and controlled navigation using the cursor keys on a keyboard. Participants moved around the octagonal exploration arena for two 30 s trials. Following these exploration trials, participants pressed enter to begin the 24 trials of stage 1 training, which were administered in the same manner as reported for Experiments 4-6. Consequently, participants began each trial at a point located halfway between the apex and obtuse corner in the kite-shaped arena, and the direction in which participants began facing was randomised for every trial. Again, there was no time limit on any trial, and participants received the same feedback when they found the hidden goal. Finally, 24 different trials were generated by presenting every possible configuration of four landmarks in the four corners of the kite-shaped arena to each participant. The order in which these trials were presented was randomized for each participant independently.

During stage 1, participants in the shape-relevant group received identical training to group shape-shape of Experiments 5 and 6a. Consequently, the goal was located in the same corner of the kite-shaped arena on each trial. The location of the hidden goal was counterbalanced across participants within this group, such that each corner of the kite signalled the goal location for three participants during the experiment. Each of the 4 blue spheres was located in the goal corner on 6 trials, and in non-goal locations on the remaining 18 trials. Similarly, participants in landmark-relevant group received identical stage 1 training to group landmark-landmark of Experiments 5 and 6a. Consequently, the goal was located under the same blue sphere on each trial. The location of the hidden goal was, again, counterbalanced across participants within this group, such that each of the blue spheres signalled the goal location for three participants during the experiment. Each of the 4 corners contained the goal on 6 trials, and did not contain the goal on the remaining 18 trials.

Having completed 24 training trials in the kite-shaped arena, participants completed stage 2 of the experiment in a trapezium-shaped arena. stage 2 consisted of 16 training trials, and three conflict test trials. In both training and test, participants began at a point half way along a notional line from the centre of the shortest wall to the centre of the longest wall. The direction in which participants began facing was randomised on each trial. Figure 4.1 shows the position of the four red landmarks in the corners of the trapezium arena during training trials. As with stage 1, the location of the hidden goal was counterbalanced across participants within each group, such that it was in each corner of the trapezium an equal number of times over the entire experiment. As the red spheres did not move during stage 2 training, this also meant that each red sphere signalled the goal location for three participants during the experiment.

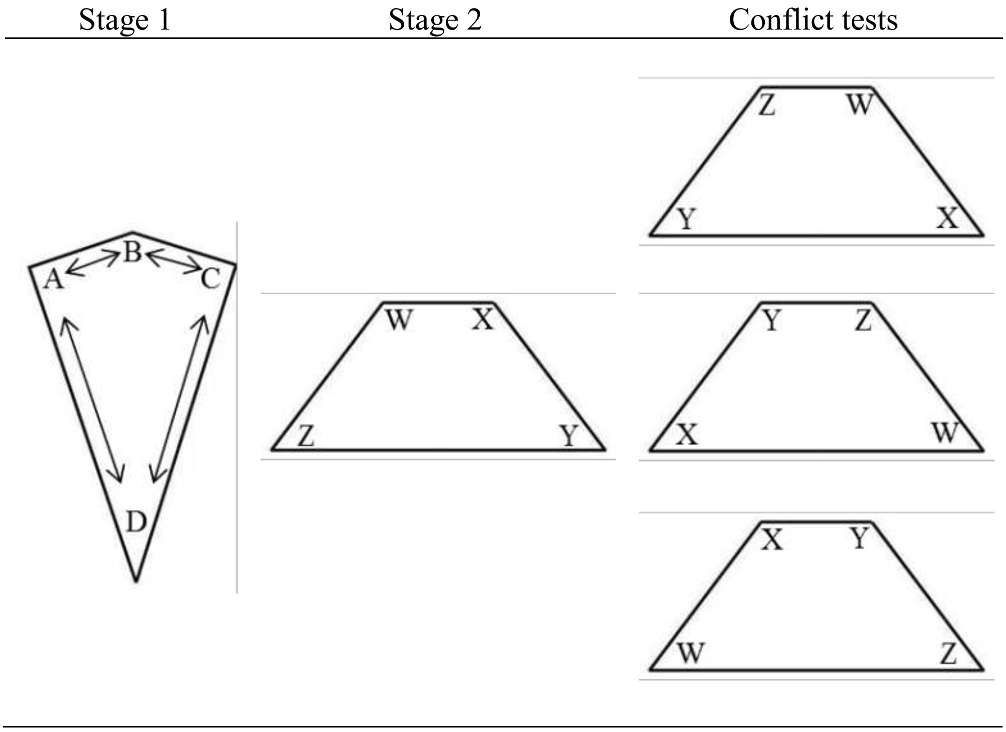

Stage 1 Stage 2 Conflict tests

Figure 4.1. Schematic diagrams of the arenas utilised in Experiment 7. A, B, C and D represent the blue spheres that were present within the kite-shaped arena during stage 1, and the arrows between them represent the fact that the landmarks moved between each of the 24 trials of stage 1 training. For the landmark-relevant group, the hidden goal remained by a particular sphere, regardless of which corner that sphere was in. For the shape-relevant group, the hidden goal remained in the same corner of the kite, regardless of which sphere was in that corner. W, X, Y, and Z represent the red spheres that were present within the trapezium-shaped arena. The red spheres remained in a constant position during training, such that for every participant, both the corner of the trapezium and the landmark located at that corner signalled the goal location. Finally, during the three test trials, the configuration of red spheres was rotated to place shape and landmark information into conflict.

Three 60-second test trials, in which the hidden goal was removed from the arena, were administered after the 8th, 12th, and 16th trial of stage 2. On each test trial, the shape and landmark cues were placed into conflict. This was achieved by rotating the configuration of the four red landmarks relative to the boundary, such that each landmark occupied a different corner to that from stage 2 training. Rotating the configuration of landmarks by one, two, or three corners in a clockwise direction produced three test trials for each participant (see Figure 4.1). The order of these test trials was counterbalanced across participants such that the one corner, two corner, and three corner rotations were administered equally often during the first, second, or third test trial during the experiment. After 60 seconds of the test trial had elapsed, participants received a message (*Press enter to start the next trial*), and the next training trial began. As with Experiment 2, square search zones that were three times the area of the hidden goal were used to measure time spent searching near the correct landmark or near the correct corner during each test trial.

4.1.2 Results

4.1.2.1 Stage 1

Figure 4.2 shows that mean latency to find the goal, in seconds, for participants in the shape-relevant and landmark-relevant groups during stage 1 of Experiment 7. In both groups, the latency to find the goal decreased across the 24 training trials, and there was also an indication that the shape-relevant group found the goal quicker in the kite than the landmark-relevant group. A two-way ANOVA of individual latencies, with a between-subject variable of group (landmark-relevant or shape-relevant), and a within-subject variable of trial (1-24), confirmed these impressions. There was a significant main effect of trial, $F(23, 506) = 26.71$, $MSE = 129.31$, $p < .001$, $\eta_p^2 = .55$, and group, $F(1, 22) = 13.90$, $MSE = 399.79$, $p = .001$, $\eta_p^2 = .39$, but there was no interaction between trial and group, $F(23, 506) = 1.27$, $MSE = 129.31$, $p = .18$, $\eta_p^2 = .05$.

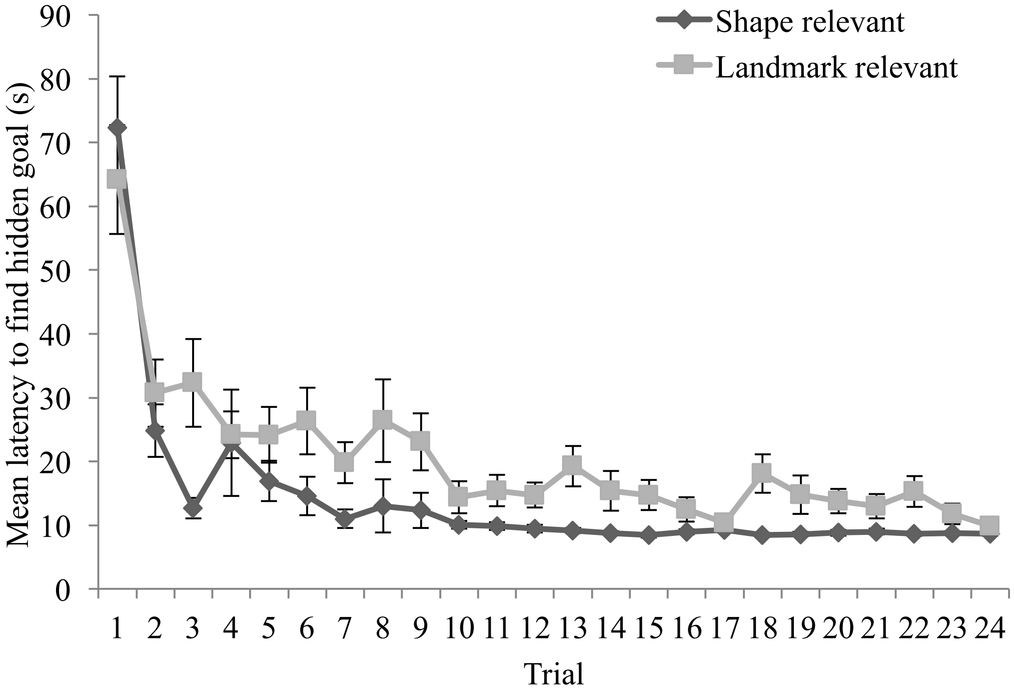


Figure 4.2. Mean latencies of the two groups to find the hidden goal in stage 1 of Experiment 7. Error bars show 1 +/- standard error of the mean.

4.1.2.2 Stage 2

Figure 4.3 shows participants' mean latency, in seconds, to find the goal in stage 2. Again, the latency to find the goal decreased across the 16 training trials in the trapezium. There was also an indication that the landmark-relevant group found the goal quicker across the course of the experiment than the shape-relevant group. These impressions were again confirmed by a two-way ANOVA conducted on individual latencies to find the goal, with a between-subjects variable of group (landmark-relevant or shape-relevant), and a within-subjects variable of trial (1-16). There was a significant main effects of trial, $F(15, 330) = 19.86$, $MSE = 62.10$, $p < .001$, $\eta_p^2 = .47$, and group, $F(1, 22) = 6.87$, $MSE = 232.86$, $p=.016$, $\eta_p^2 = .24$, but no interaction between these variables, $F(15, 330) = 1.31$, $MSE = 62.10$, $p= .20$, $\eta_p^2 = .06$.

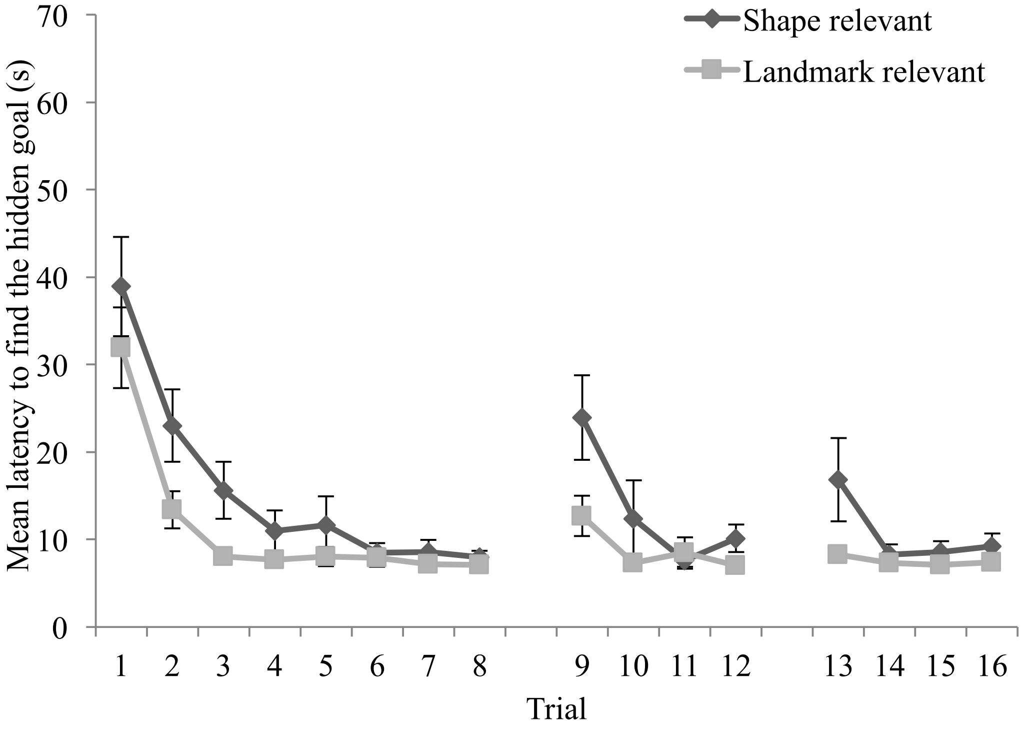


Figure 4.3. Mean latencies of the two groups to find the hidden goal in stage 2 of Experiment 7. Error bars show 1 +/- standard error of the mean.

4.1.2.3 Test trials

Figure 4.4 displays the time spent searching in the landmark and shape zones during the three tests by participants in the shape-relevant and landmark-relevant groups, respectively. The landmark zone was located under the landmark cue that had signalled the goal location and, similarly, the shape zone was located in the corner of the trapezium-shaped environment that had signalled the goal location. Participants in the shape-relevant group spent more time in the shape than the landmark zone during all three tests. The opposite pattern of results was observed for the landmark-relevant group. Here, participants spent longer searching in the landmark zone, compared to the shape zone, during the three tests. In both groups, the bias for searching in one zone over another became stronger in later tests. A three-way ANOVA of individual time spent in zones, with the between-subject variable of group (shape-relevant or landmark-relevant), and within-subject variables of zone (shape or landmark) and test (first, second, or third), revealed no significant main effects of group, $F(1, 22) = 2.32$, $MSE = 40.66$, $p = .14$, $\eta_p^2 = .10$, zone, $F(1, 22) = 2.67$, $MSE = 63.29$, $p = .12$, $\eta_p^2 = .11$, or test, $F(2, 44) = 1.33$, $MSE = 6.97$, $p = .28$, $\eta_p^2 = .06$. There was no significant interaction between test and group, or between test and zone, Fs<1. There was, however, a significant interaction between group and zone, $F(1, 22) = 16.18$, $MSE = 63.29$, $p = .001$, $\eta_p^2 = .11$, as well as a significant three-way interaction between group, zone, and test, $F(2, 44) = 3.51$, $MSE = 13.18$, $p = .038$, $\eta_p^2 = .14$. The simple main effects of the three-way interaction that are crucial to the hypotheses regard the time spent in the landmark and shape zones *within* the shape-relevant and landmark-relevant groups, and so *between* group effects are not reported. Taking the shape-relevant group first, participants did not show a significant preference for searching in the shape zone over the landmark zone during the first, $F<1$, or second test trials, $F(1, 22) = 1.25$, $p = .28$, $\eta_p^2 = .05$; however, the shape-relevant group did display a preference for searching in the shape zone over the landmark zone during the third test, $F(1, 22) = 5.09$, $p = .034$, $\eta_p^2 = .19$, $\eta_p^2 = .05$. For the landmark-relevant group, participants displayed a significant preference for searching in the landmark zone over the shape zone on each test trial, Fs$(1, 22) > 7.08$, ps$< .014$, $\eta_p^2 > .24$.

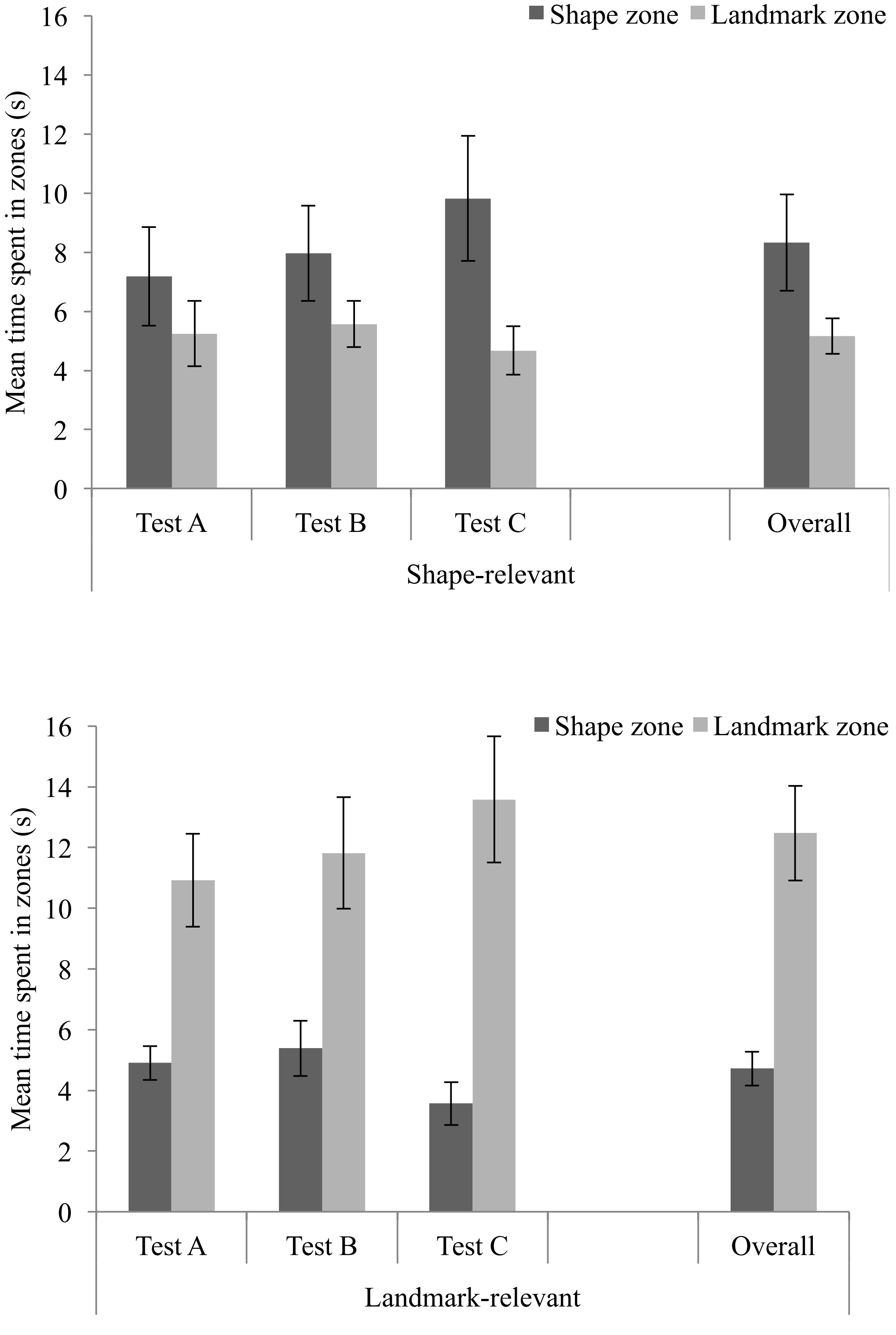


Figure 4.4. Mean time spent in zones for each of the three conflict tests of Experiment 1 for the shape (top) and landmark (bottom) relevant groups. Error bars represent 1+/- standard error of the mean.

4.1.3 Discussion

Experiment 7 showed that, by establishing a particular cue dimension as relevant to navigation, it is possible to bias which cue dimension will dominate search behaviour when these two dimensions are subsequently established as equivalently relevant cues for a navigational goal. During the conflict tests administered during stage 2, participants who had received landmark-relevance training in stage 1 of the experiment searched near the landmark more than they did the corner of the trapezium. In contrast, during the same conflict tests, participants who were given shape-relevance training in stage 1 of the experiment searched near the corner more than they did near the landmark. Importantly, these biases emerged despite both the shape of the arena, and the landmarks within it, being equally relevant as cues for the location of the hidden goal during stage 2. Furthermore, as conflict tests were used to assess the relative dominance of the competing cues, in which all the cues employed during training were still presented to participants at test, it is difficult to explain these data by appealing to generalisation decrement in its simplest form.

It was evident that the predictiveness training administered in stage 1 of the experiment produced a stronger effect in the landmark-relevant group than it did in the shape-relevant group. This may be due to the group difference that was noted in stage 1 of the experiment, in which participants in the shape-relevant group learned to locate the goal quicker than did participants in the landmark-relevant group. In the navigational task used in the current experiments, participants controlled what non-reinforced stimuli, if any, were encountered before the goal was found (see Miller & Shettleworth, 2007), which raises the possibility that participants in the shape-relevant group may have sampled a restricted number of non-reinforced stimuli relative to participants in the landmark-relevant group. Consequently, at the onset of stage 2, the shape cues may have been less relevant for the shape-relevant group than were the landmark cues for the landmark relevant group. An alternative explanation for the stronger effect that was noted in the landmark-relevant group might be that the landmark cues in the trapezium were, unconditionally, more salient than the shape properties provided by the boundary walls. If this was the case, landmark-relevance training during stage 1 of the current experiment would only serve to enhance a pre-existing difference in salience. For the shape-relevant group, the training given in stage 1 should ensure than the attention paid to the shape properties of the boundary walls was higher than the attention paid to the landmark cues at the onset of stage 2. This manipulation, however, may have been somewhat counteracted by the fact that the landmark cue was, unconditionally, much more salient than the shape information provided by the boundary walls of the trapezium. It is difficult to evaluate this possibility without having a measure of baseline performance. Experiment 8 was conducted to gain this measure of baseline performance.

4.2 Experiment 8

Participants in the no pre-training group received training identical to that administered in stage 2 of Experiment 7. Participants could, therefore, rely on either the shape information provided by the boundary walls of the trapezium, or the landmarks within it, to locate a hidden goal. Again, three conflict tests were administered, in which the landmark cues were placed into conflict with the shape information provided by the boundary walls. If the landmark cues within the trapezium are more salient than the shape information provided by the boundary walls, then participants should spend more time searching near the landmark that had previously signalled the goal location compared to the time spent searching in the corner of the trapezium that had signalled the goal location. In contrast, if the shape information provided by the boundary walls is more salient than the landmark cues, participants should spend more time searching near the corner of the trapezium that had signalled the goal location, than the landmark. Finally, if both cue dimensions are of equal salience, then participants would be expected to spend equal amounts of time searching by the corner of the trapezium that had signalled the goal location and by the landmark that had signalled the goal location.

In addition, a pre-training group who received identical training within the trapezium environment was also included; however, this was preceded by training in a kite-shaped arena. In contrast to Experiment 7, both the shape properties provided by the boundary walls, and the landmarks contained with the arena, were established as equally relevant for finding the goal. This was achieved by keeping the relationship between the spherical landmarks, the arena corners, and the hidden goal constant on each trial. By including this group, it was possible to better match the training in stage 1 with the two groups of Experiment 7; thus, ensuring that participants enter stage 2 having had experience of navigating in the kite-shaped environment. Attentional theories of associative learning differ in their prediction of the effect of compound training on the salience of the individual cues. According to Mackintosh (1975, see also Esber & Haselgrove, 2011) such training will amplify any unconditional difference in salience between the cues. This follows because attention to a cue will increase if it is the best available predictor of the outcome (in this case the hidden goal), and decrease if it is not. Early on in training the more salient cue in a compound will enter into an association with the hidden goal quicker than the less salient cue. Consequently, the more salient cue will gain more attention, and the baseline, unconditional, difference in salience between the cues will increase. In contrast, Pearce and Hall (1980) predict that the effect of compound training will be to, at best, sustain any unconditional difference in salience between the cues and, at worst, attenuate their difference. This follows because Pearce and Hall proposed that attention to *each* cue in the compound is equal to the (absolute) total prediction error from the previous trial. As this prediction error will diminish as training progresses, so too will attention to each cue, until they reach an equivalent, low, level. In any case, these theories do not predict that the effect of compound training will be to reverse any differences in the unconditional salience of cues trained in compound and, on this basis, the pre-training group should permit an uncompromised measure of cue salience.

As well as allowing for a measure of baseline performance on the navigation task, which is necessary in order to accurately interpret the data obtained from Experiment 7, Experiment 8 was also theoretically motivated. Previous studies have demonstrated that when boundary and landmark information are established as equally predictive of a goal and then subsequently placed in conflict, the boundary cues control navigational behaviour. As previously mentioned, Cheng (1986) trained rats to find food that was buried in a particular corner of a rectangle-shaped arena, the corners of which contained a unique landmark. In one version of his task, Cheng moved the previously relevant landmark to an incorrect geometric corner - placing the boundary shape and landmark cues into conflict. Under these circumstances, rats chose to search in the location signalled by the previously relevant geometry, rather than the location signalled by the previously relevant landmark. Similar findings have also been noted in human adults tested in a real world circular environment that was orientated by two boundary cues, and that contained an intramaze landmark (Bullens et al., 2010). These findings are consistent with theories that propose that information provided by the boundary shape of an environment should control navigational behaviour, even in the presence of equally relevant cues (e.g. Gallistel, 1990). When viewed in the context of this empirical and theoretical precedent, therefore, it would be particularly surprising if the landmark cues unconditionally controlled navigational behaviour, at the expense of boundary cues.

4.2.1 Method

4.2.1.1 Participants

24 participants were recruited from the University of Nottingham (18 female). Participants were allocated randomly to either the no pre-training or pre-training groups, with the restriction that an equal number of male and females were distributed between the two groups. Participants were again given course credit or £5 in return for participation. The age of participants

ranged from 18 to 40 years (mean = 20.88, *SD* = 4.86). An additional £10 was awarded to the participant who completed stage two of the experiment in the shortest time.

4.2.1.2 Materials

All material details were the same as described for Experiment 7.

4.2.1.3 Procedure

All procedural details, including details pertaining to the exploration arena, were the same as described in Experiment 7. The no pre-training group received training and conflict tests that were identical to those described for stage 2 of Experiment 7. The pre-training group also received these trials, but were first required to complete 24 trials in a kite-shaped arena that contained the same four blue landmarks as detailed in Experiment 7. During these 24 trials, the location of the hidden goal was signalled by both the shape properties provided by the boundary walls of the arena, and the landmarks contained within the arena. For all participants in the pre-training group, the hidden goal was located in the right angled corner of the kite where the left wall was shorter than the right wall. The landmarks within the arena remained static for each participant; however, the location of the landmarks was counterbalanced across subjects, such that each blue landmark (A, B, C, and D – see Figure 4.1) signalled the goal location for three different participants during the experiment.

4.2.2 Results

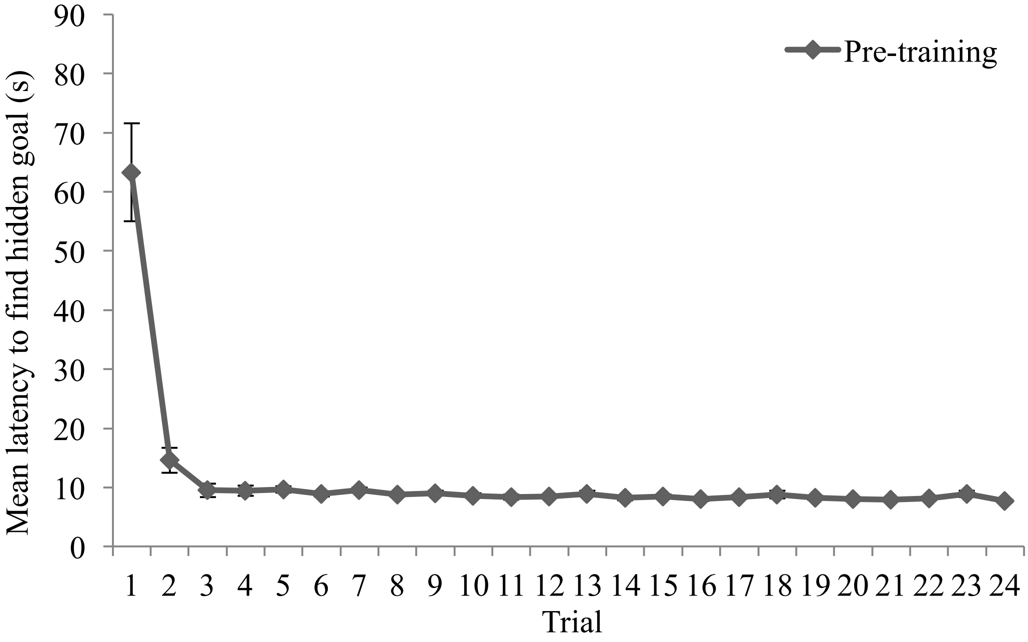
Mean latencies to find the hidden goal during the acquisition trials for participants in the no pre-training group are analysed together with stage 2 mean latency data for participants in the pre-training group.

4.2.2.1 Stage 1

The top panel of Figure 4.5 shows that the mean latency, in seconds, for participants in the pre-training group to find the goal during stage 1 of the experiment decreased across the 24 training trials in the kite. A one-way ANOVA of individual latencies, with a within-subjects variable of trial (1-24), confirmed this impression, $F(23, 253) = 40.13$, $MSE = 37.38$, $p < .001$, $\eta_p^2 = .79$.

4.2.2.2 Stage 2

The bottom panel of Figure 4.5 shows the mean latency, for participants in both the no pre-training and pre-training groups, to find the goal in stage 2 of the experiment. Again, the latency to find the goal decreased across the 16 training trials in the trapezium. It was also evident that the pre-training group found the goal quicker than the no pre-training group on early trials. A two-way ANOVA conducted on individual latencies to find the goal, with a between-subject variable of group (no pre-training or pre-training), and a within-subject variable of trial (1-16), revealed significant main effects of trial, $F(15, 330) = 18.14$, $MSE = 101.02$, $p < .001$, $\eta_p^2 = .45$, group, $F(1, 22) = 5.62$, $MSE = 334.35$, $p = .027$, $\eta_p^2 = .20$, and a significant interaction between trial and group, $F(15, 330) = 3.93$, $MSE = 101.02$, $p < .001$, $\eta_p^2 = .15$. Simple main effects analysis revealed that the pre-training group were quicker to find the goal on trial 1 only, *F*(1, 22) = 9.93, *MSE* = 588.31, *p*=.005, η_p^2 = .31.



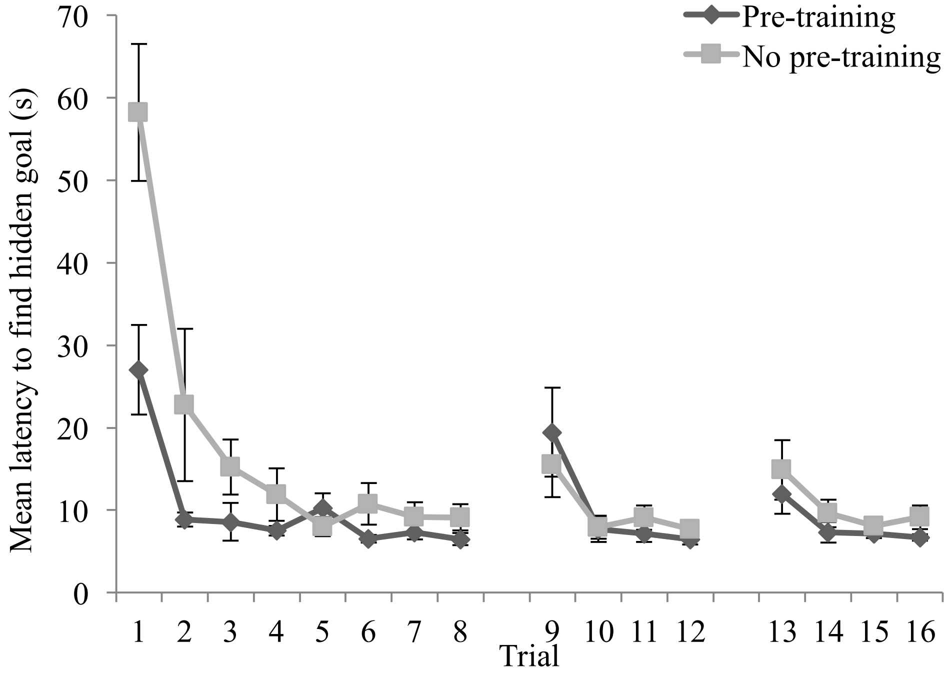
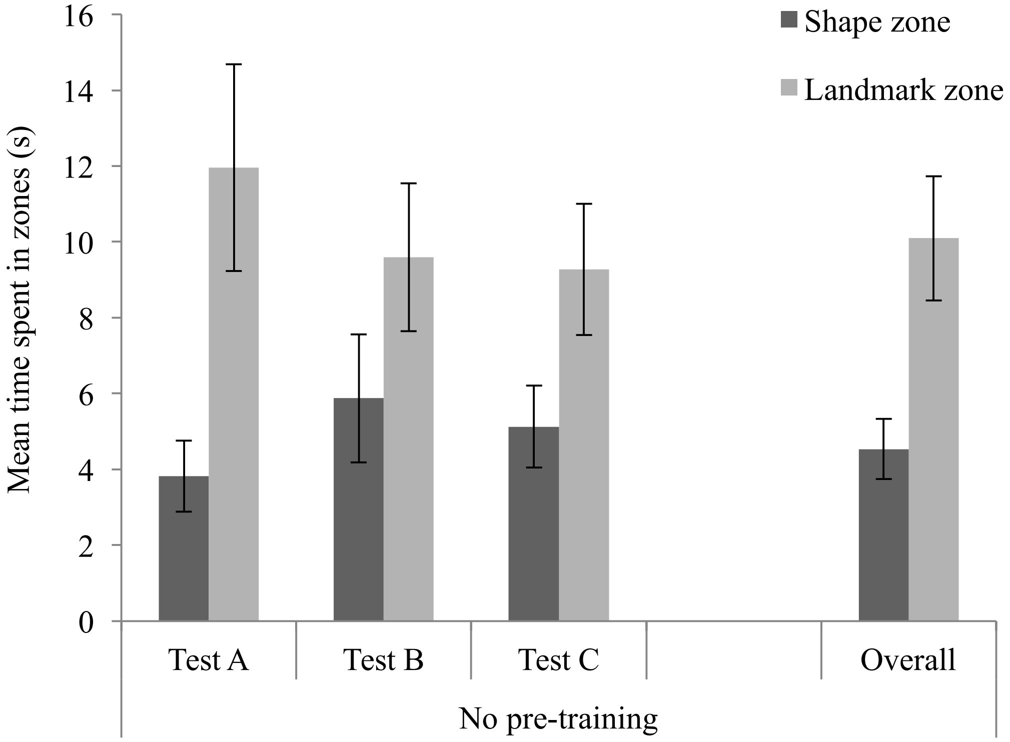


Figure 4.5. Mean latency for group pre-training to find the hidden goal in stage 1 (top), and groups pre-training and no pre-training to find the hidden goal in stage 2 (bottom), of Experiment 8. Error bars show 1 +/- standard error of the mean.

4.2.2.3 Test trials

Figure 4.6 displays, in seconds, the time spent searching in the landmark and shape zones during the three tests of the experiment by participants in the no pre-training and pre-training groups. Participants in the no pre-training group spent more time searching in the landmark zone, over the shape zone, during the three tests, although this preference for the landmark zone appeared to weaken over the tests. Participants in the pre-training group appeared to initially spend more time searching in the landmark zone over the shape zone. Again, though, this preference weakened over tests, and did not appear present during the third test. Despite these observations, a three-way ANOVA of individual time spent in zones, with a between-subject variable of group (no pre-training or pre-training), and within-subject variables of zone (shape or landmark) and test (first, second, or third), revealed only a significant main effect of zone, $F(1, 22) = 9.81$, $MSE = 54.09$, $p=.005$, $\eta_p^2 = .31$, indicating that all participants spent more time searching in the landmark zone compared to the shape zone. The main effects of group and test were not significant, both Fs<1, nor were the interactions between test and group, $F<1$, zone and group, $F(1, 22) = 1.50$, $MSE = 54.09$, $p= .23$, $\eta_p^2 = .06$, as well as test and zone, $F(2, 44) = 1.62$, $MSE = 23.16$, $p= .21$, $\eta_p^2 = .07$. Finally, the three-way interaction was not significant, $F<1$.



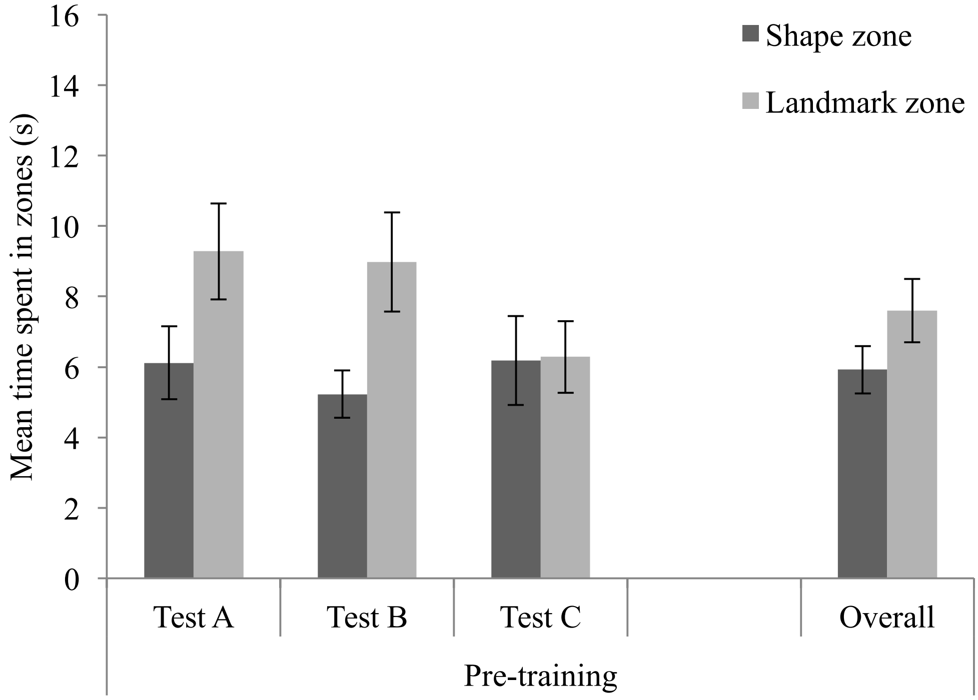


Figure 4.6. Mean time spent in zones for each of the three conflict tests of Experiment 8 for the No pre-training (top) and Pre-training (bottom) groups. Error bars represent 1+/- standard error of the mean.

4.2.3 Discussion

During the conflict tests, the no pre-training group of Experiment 8, searched for longer near the landmark cue that previously signalled the goal location, compared to near the corner of the trapezium arena that previously signalled the goal location. As hypothesised, when the shape information provided by the boundary walls of a trapezium arena, and the landmarks within the arena, are placed into conflict, the landmark cues dominated behaviour – a result that is assumed to reflect the greater unconditional salience of the landmark cue, relative to the shape information provided by the boundary walls of the environment. A similar pattern of results was also observed in the data obtained from the pre-training group. Again, participants searched for more time near the landmark cue than they did near the correct corner of the trapezium. It appeared that the main effect of zone was carried largely by the no pre-training group. Numerically, at least, the preference for searching near the landmark cue at test was attenuated in the pre-training group, compared to the no pre-training group. Incidentally, this result is consistent with a model of attentional learning that employs a summed error term to determine the attention paid to cues (e.g. Pearce & Hall, 1980); however, it must be noted that there was not an interaction within the data to substantiate this claim.

That participants favoured searching near the landmark cues, over the boundary cues, contrasts with previous empirical evidence that boundary cues control navigational behaviour in the presence of equally predictive landmark information (e.g. Bullens et al., 2010; Cheng, 1986). Furthermore, it seems difficult to explain these results with theories which suggest that information provided by the boundary shape of an environment should control navigational behaviour, even in the presence of equally relevant cues (e.g. Gallistel, 1990). It may, however, be possible to explain instances where boundary information has dominated navigational behaviour over landmark information, or vice versa, by appealing to associative learning theories that allow for changes in the attention paid to salient stimuli. To avoid undue repetition, this is elaborated on this further in the general discussion.

4.3 General Discussion

Experiment 7 showed that it is possible to manipulate which cue dimension would take control of navigational behaviour in a trapezium-shaped arena that also contained landmarks, by preceding exploration of this environment with relevance training in a different-shaped arena, which contained different landmarks. The shape information provided by the boundary walls of the environment took control of behaviour if participants had received shape-relevance training prior to learning the goal location in the trapezium. In contrast, the landmark cues within the trapezium took control of behaviour if participants had received landmark-relevance training prior to learning the goal location in the trapezium environment. The effect of relevance training appeared to be asymmetrical, with a greater bias in exploration in the landmark-relevant group. On the basis of this, it was proposed that the unconditional salience of the landmarks was greater than the shape properties provided by the trapezium, and Experiment 8 confirmed this. When learning in the trapezium was preceded by no relevance training altogether, or training in which both shape and landmark cues were relevant, the landmark cues contained within the trapezium took control of behaviour.

The data presented here are inconsistent with theories that suggest that learning about shape information occurs in an impervious geometric module (e.g. Cheng, 1986; Gallistel, 1990; Wang & Spelke, 2002, 2003), as these theories do not permit learning about landmark information to interact with learning about information provided by boundary walls. Furthermore, the results presented here are also inconsistent with the associative model of spatial navigation proposed by Miller and Shettleworth (2007, 2008, 2013), as this theory employs a Rescorla-Wagner (1972) learning algorithm (and a choice rule) to determine approach behaviour during spatial navigation. In Experiment 7, an entirely different set of stimuli were used in stage 2 to those employed during training in stage 1 and, consequently, any associative strength acquired by the stimuli during training would not directly transfer to the stimuli employed in stage 2 – negating the possibility of them influencing behaviour. Even if generalization of associative strength is permitted between the stimuli used in stage 1 and stage 2, this would still not systematically bias search behaviour as the stimuli that were employed as signals for the presence *and absence* of the hidden goal in stage 1 were established (through appropriate counterbalancing) as equivalently similar to the stimuli that signalled the goal location during stage 2. Consequently, any propensity for generalization to promote search behaviour near one particular stimulus would be exactly balanced by its propensity to inhibit the same behaviour.

The learned predictiveness effects presented here are, however, consistent with associative models that allow for changes in the attention paid to relevant and irrelevant stimuli (e.g. Esber & Haselgrove, 2011; Mackintosh, 1975). To reiterate, these theories suggest that stimuli (and by generalisation, stimulus dimensions) that are the best predictors of an outcome will gain an increase in their attention, whereas stimuli (or stimulus dimensions) that are poor predictors of an outcome will suffer a reduction in their attention. On the basis of this, it is possible to understand the results from Experiment 7. As participants navigational behaviour was unconditionally biased towards using the landmark cues in stage 2 (Experiment 8), administering landmark-relevance training in stage 1 served to further increase, through generalisation, the salience of landmarks contained within the trapezium further, as well as decrease the salience of shape information provided by the boundary walls of the trapezium. This unconditional bias in salience was, seemingly, overcome by the stage 1 training in the shape-relevant group. For these participants, attentional theories predict that the initially salient landmarks will suffer a loss in attention as they are established as irrelevant to navigating towards the goal, and attention to the goal-relevant shape cues will increase. If sufficient training is given, this training should overcome any unconditional biases in salience and, again through generalisation, transfer to the cues employed in stage 2 – permitting the establishment of a bias towards learning about the shape of the arena.

It was previously noted that the results from the test trials of Experiment 8 were, at least numerically, consistent with the model of learning proposed by Pearce and Hall (1980). It may, however, be possible to reconcile the results of Experiment 8 with the attentional model of learning proposed by Mackintosh (1975). In Experiment 8, it was observed that that the red landmarks contained within the trapezium-shaped environment were more salient than the shape information provided by the boundary walls of the arena (no pre-training group). This finding is consistent with the observation that, in stage 2 of Experiment 7, the landmark-relevant group learned the task quicker than participants in the shape-relevant group. Participants in the shape-relevant group of Experiment 7, however, learned the task quicker than participants in the landmark-relevant group during stage 1. It might, therefore, be suggested that the shape information provided by the kite-shaped environment was more salient than the landmarks contained within it. This notion gains a measure of support from the results observed in the pre-training group of Experiment 8. According to Mackintosh (1975), if it is assumed that the shape information of the kite-shaped arena is more salient than the landmark cues within it, then the associative strength of the shape information should be stronger than the associative strength of the landmark information at the end of stage 1 training. Importantly, this effect that will be mirrored by the attention paid to these different cues, and these differing levels of attention will generalise to the novel stimuli, taken from the same stimulus dimension, that were presented in stage 2. Stage 1 training in the pre-training group, therefore, would serve to counteract the unconditional higher salience of the landmark cues present in stage 2, relative to the shape information provided by the boundary walls. Consequently, it would be expected that the pre-training group should demonstrate an attenuated preference for searching near the landmark cue during stage 2 test trials, relative to the no pre-training group. As the landmark cues were still relevant in stage 1 training for the pre-training group, however, it would not be expected that stage 1 training for this group would completely counteract the unconditional salience of the landmark cues in stage, as was observed in the shape-relevant group of Experiment 7.

The current results provide a proof of concept to the idea that the differing results of spatial overshadowing experiments can be accounted for by the relative salience of landmark and boundary wall cues. Following Mackintosh (1975), it is possible that failures of a landmark to overshadow a boundary shape (e.g. Doeller & Burgess, 2008), and instances in which boundary information has dominated behaviour over landmark information (e.g. Bullens et al., 2010; Cheng, 1986), may be due to the landmark possessing low unconditional salience relative to the shape. Likewise, successes of landmarks overshadowing boundary shape (e.g. Pearce et al., 2006), and instances where landmark cues have dominated navigational behaviour over boundary cues (Experiment 8), may be due to the landmark possessing high unconditional salience relative to the shape. One further possibility raised by attentional theories of learning is that failures of landmarks to overshadow learning about information provided by boundary walls may not be limited to instances of salience asymmetry. Mackintosh (1976) noted that, if both cues enter an experiment with particularly high unconditional salience, then they will be limited in their ability to undergo a further increase in attention. This will have the consequence of permitting them to acquire an equivalent association with the trial outcome as a cue that is trained in isolation; thus, limiting the degree to which overshadowing can be observed. Consequently, if both the landmark and shape cues in previous overshadowing experiments were both of an unconditionally high salience, then the landmark would fail to overshadow learning based upon the shape of the boundary, and vice versa. Evidence consistent with this general prediction about the influence of stimulus salience on overshadowing was obtained in a non-spatial learning experiment reported by Mackintosh (1976), who demonstrated that overshadowing of conditioned suppression in rats was obtained between two stimuli when they were both of a low unconditioned salience, but not when they were both of a high unconditional salience. It remains to be determined whether a comparable effect can be observed in the spatial domain.

It is relevant, at this point, to discuss the results in relation to empirical data gathered from other spatial learning experiments. The findings are consistent with overshadowing studies in which a landmark has successfully overshadowed learning about the shape properties provided by the boundary walls of an environment (Cole et al., 2011; Horne et al., 2010; Horne & Pearce, 2011; Pearce et al., 2006). A similar effect was observed in Experiment 8, where landmarks dominated behaviour over the shape properties provided by the boundary walls of the arena. However, this was observed by comparing performance in a direct manner via a series of conflict tests, rather than via a traditional overshadowing design, in which navigation using only the boundary walls of the environment is compared following either landmark-boundary wall compound training, or training with just the boundary walls alone. The conflict tests employed here measure what cue has taken control over behaviour when the confounding effects of generalisation decrement are less apparent. Of more theoretical importance, the results gathered here complement experimental data gathered from rats (Kosaki et al., 2013) and extend the findings to human participants. In their experiment, Kosaki et al. demonstrated that the obtuse corners of a rhombus were less salient than the acute corners, before demonstrating that discrete landmarks were able to overshadow the less salient obtuse corner, but not the more salient acute corner. Taken together, the results of Experiment 7 and those of Kosaki et al. (2013), suggest that spatial cues of superior salience take control of navigational behaviour in a manner that is partially consistent with the predictions made by associative theories of navigation (e.g. Miller & Shettleworth, 2007, 2008, 2013). Importantly, though, the current results are consistent with the ID-ED experiments presented in Chapter 3 and, along with the findings reported by Cuell et al. (2012), suggest associative models of spatial navigation need to acknowledge the role of more top-down attentional process. That is, associative models must permit changes in the attention paid to a stimulus to be driven both by the inherent properties of that stimulus (bottom-up), and also by more central changes in attention that are a consequence of learning about that stimulus (top-down), as proposed by attentional models (e.g. Esber & Haselgrove, 2011; Le Pelley, 2004; Mackintosh, 1975).

4.3.1 Conclusion

The experiments reported here, together with overshadowing experiments such as those reported by Kosaki et al. (2013), suggest that the same associative processes that explain learning in the non-spatial literature may also explain spatial learning phenomena. Associative theories are able to explain successful observations of cue competition effects between shape information provided by boundary walls and landmark cues, an experimental phenomenon that is inconsistent with theories that state that shape information provided by the boundary walls of an environment is learned about independently from landmark cues (e.g. Cheng, 1986; Gallistel, 1990; Wang & Spelke, 2002, 2003), or those which state this information is learned about in a manner inconsistent with associative learning theories (e.g. Doeller & Burgess, 2008). More importantly, considering the continued importance of modular theories (e.g. Gallistel & Matzel, 2013; Spelke & Lee, 2012; Jeffrey, 2010), the development of associative accounts of spatial navigation that incorporate an attentional variant will provide the necessary framework to explain the absence of overshadowing between landmarks and shape information, without recourse to specialised processing of certain cues.

Chapter 5

Human spatial-navigation requires multiple representations of the shape of the environment

As reviewed in Chapter 1, a number of navigational theories propose that organisms encode a global representation of the shape of the environments in which they navigate (e.g. Cheng, 1986; Wang & Spelke, 2002, 2003). For instance, according to Gallistel (1990), animals encode a cognitive map that represents only the Euclidean shape of the environment (p. 220). Under this proposal, animals encode a representation of the entire shape of their environment in which both the distance and angular information provided by the boundary walls are preserved and, moreover, animals also acquire a sense of the relative positions of the different length walls that create the environmental boundary (see Lee, Sovrano, & Spelke, 2012; Spelke & Lee, 2012).

The notion that organisms navigate using a Euclidean representation of the shape of the environments was challenged by a number of shape-transformation experiments that demonstrated that animals can transfer navigational behaviour based on local-shape information between environments that have a different global-shape. Specifically, it has been shown that organisms can transfer navigational behaviour that is based upon information provided by the lengths of wall configurations (e.g. Lew et al., 2014; McGregor et al., 2006; Pearce et al., 2004; Poulter et al., 2013: See also Experiment 1 of this thesis), and the angles created where two walls join together (e.g. Lubyk et al., 2012; Tommasi & Polli, 2004). Such findings have led a number of authors to question whether organisms learn about a global representation of the shape of the environment in which they navigate (e.g. Pearce 2009, Twyman & Newcombe, 2010). As seen in Chapter 1, the navigational theory proposed by Miller and Shettleworth (2007, 2008, 2013) rules out this possibility, as it only permits changes in the associative strength to local elements.

It is important to note that evidence implicating navigation on the basis of local-shape information does not constitute evidence against the possibility of also encoding global-shape information. For instance, in the first stage of the experiment conducted by Pearce et al. (2004), it is possible that animals used both the local- and the global-shape properties of the kite-shaped environment to navigate to the hidden goal. At test, the global representation of the kite-shaped training environment would be incongruent to the, now, rectangle-shaped test environment. Consequently, any global representation encoded by rats during training would be of little worth in guiding navigation during test; thus, forcing them to navigate on the basis of the local-shape information that was preserved between the training and testing environments. Given this argument, there is little evidence against claims that organisms encode a global representation of the shape of the environments they navigate in (Cheng, 1986; Gallistel, 1990). At the same time, however, there is surprisingly little behavioural evidence to support these claims, despite their continued discussion in the navigational literature (e.g. Burgess, 2006, 2008; Gallistel & Matzel, 2013; Lew, 2011; Spelke & Lee, 2012; Tommasi, Chiandetti, Pecchia, Sovrano, & Vallortigara, 2012), and real-world behaviours that suggest people are motivated to use a global representation of the shape of the environment. For example, when working within, around, or upon a building, maintenance workers frequently consult a blueprint, or plan view, of the building in order to acquire a global representation of its shape.

Part of the problem in dissociating global- from local-shape representations is that it is difficult to design an environment whereby navigation based on a Euclidean representation of global geometric cues can be uncoupled from navigation based on local-shape cues. One manner in which this might be achieved is by training participants on the inside of an arena, before conducting a test trial on the outside of the same-shaped arena. As noted by Lourenco and Huttenlocher (2007), local-shape information is viewpoint dependent. For example, consider an animal that is trained to navigate to the inside corner of a kite-shaped arena where a short wall is to the left of a long wall. When placed on the outside of the same arena, the view of the rewarded corner is a short wall to the right of a long wall; thus, the relative lengths of the left- and right-sided walls are reversed from training. In contrast, a global representation of the Euclidean shape of the environment is viewpoint independent, because the overall shape of an environment does not change depending on the position of the navigator.

Seemingly, only one study has conducted an inside-to-outside manipulation before. In an experiment conducted by Lourenco, Huttenlocher, and Vasilyeva (2005), 2-year old infants watched an experimenter hide a toy in a corner of a rectangle-shaped box (76.20 cm x 114.30 cm, 43.18 cm high) that was located in a circular enclosure. During this phase of the experiment, infants were either placed on the inside or outside of the rectangle-shaped box. Once the toy was hidden, infants were disorientated, and asked to find the toy from the alternative side of the arena (i.e. outside or inside, respectively). Providing the disorientation procedure occurred following the translation between inside and outside, infants were able to relocate the toy. Interestingly, infants were unable to relocate the toy if disorientation followed the translation between inside and outside. It is, however, rather difficult to interpret these results in terms of what spatial representations children may have been using to guide search behaviour. As the authors note, when outside of the rectangle-shaped box, the walls were sufficiently small that infants could view every corner of the box from one position. Consequently, when on the outside of the box, participants would still have access to the spatial information from the inside of the box. This being the case, it is not possible to dissociate responding on the basis of global- or local-shape cues.

The experiments reported in this chapter were designed to assess the extent to which local- and global-shape representations are relied upon during navigation and, more specifically, to assess whether a global representation that represents the Euclidean shape of an environment is encoded during navigation. Participants in Experiments 9a and 9b were trained to navigate to a right-angled corner where, for example, a short wall was to the left of a long wall on one side of an arena (Experiment 9a: inside; Experiment 9b: outside). Following this training, participants received a test trial conducted on the alternative side of the same-shaped arena (Experiment 9a: outside; Experiment 9b: inside). As noted previously, the relative lengths of the left and right side walls are reversed in these circumstances; thus, participants could not navigate to the goal corner on the basis of local-shape cues (Pearce et al., 2004). Navigation that is based upon a global representation of the Euclidean shape of the environment, however, would lead participants to the goal corner (e.g. Gallistel, 1990). In Experiments 10a and 10b, participants were again trained to navigate to a particular corner on one side of a kite-shaped arena, before receiving a test trial conducted on the alternative side of a rectangle. As the global-shape of the training and test environments differed, participants could not navigate to the goal corner, at test, on the basis of a Euclidean representation of the environment (e.g. Gallistel, 1990). Consequently, this manipulation assessed if participants could navigate to a previously rewarded corner on the basis of only the principal axis of the shapes, a concept that will be discussed in detail in the introduction to Experiment 10. Finally, in Experiment 11, participants were trained to navigate to a hidden goal on the outside of a kite-shaped arena before testing their search behaviour on the outside of a rectangle-shaped arena (or vice versa). This experiment assessed whether navigation around the outside of these shapes was consistent with previous observations from shape transformation experiments that have been conducted on the inside of these shapes (e.g. Lew et al., 2014; Pearce et al., 2004: see also Experiment 1).

5.1 Experiments 9a and 9b

In Experiments 9a and 9b, the hidden goals that participants were searching for were framed as Wi-Fi and mobile (cell) phone signals, respectively. Searching for such signals has considerable face validity for young participants, not least because these signals can realistically be present both on the inside and the outside of an arena, despite having an origin on only one side. In Experiment 9a, participants were trained to find a hidden goal that was positioned at one of the right-angled corners on the inside of either a kite- or rectangle-shaped virtual environment. Following this training, participants were given a single test trial in which, unbeknownst to the participants, there were no hidden goals. During the test trials, participants were placed on the outside of the same-shaped area in which they were trained, and allowed to search for 120 seconds (see Figure 5.1). If, during the test trial, participants were navigating on the basis of a Euclidean representation of the geometry of the environment (Gallistel, 1990), they should spend more time searching near the corner that previously contained the hidden goal (signal zone). If, however, participants were relying on a local solution, and searching near a corner where a short wall was to the left of a long wall, they would be expected to spend more time searching near the corner that did not previously contain the goal (no-signal zone). Experiment 9b followed the same logic, but participants were trained to find a hidden goal on the outside of a kite- or rectangle-shaped environment, before being tested on the inside of the same shape for 60 seconds in the absence of any hidden goals (Figure 5.2). As with Experiment 9a, participants were predicted to search in different corners of the test arena if they were navigating using a global strategy, compared to a local strategy.

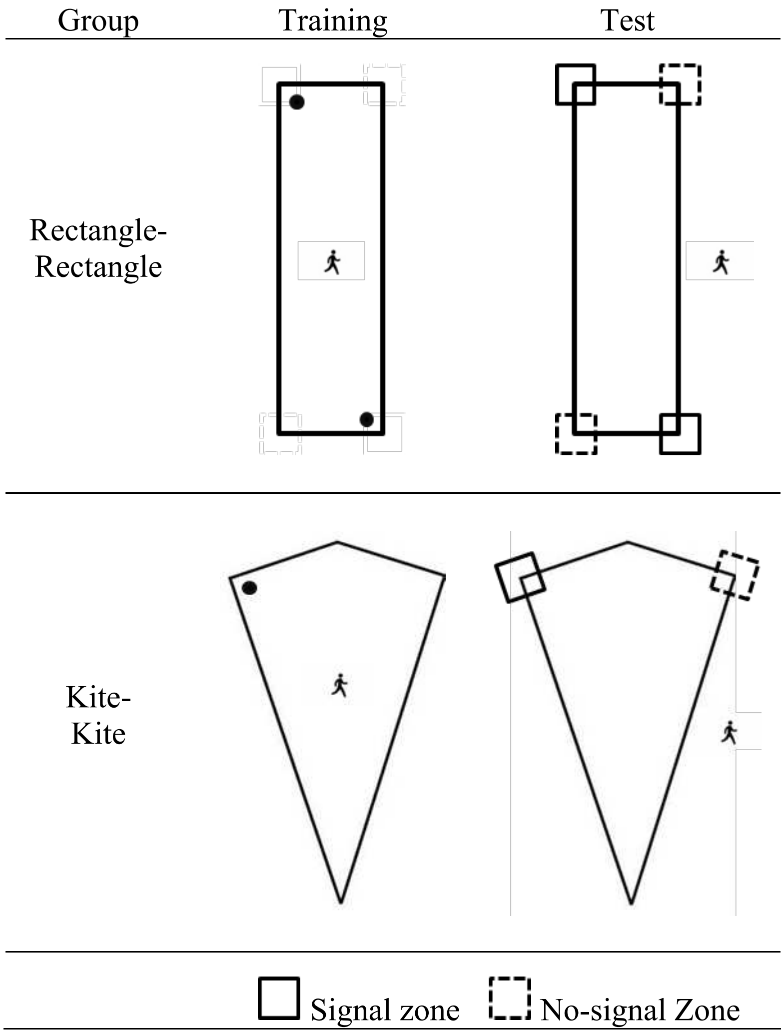


Figure 5.1. Schematic views of the training and test environments for the two groups of Experiment 9a. Black circles represent the location of a hidden goal, and square search zones are superimposed on the diagram of the test environment. The location of the person indicates whether participants were navigating on the inside, or the outside, of the arena.

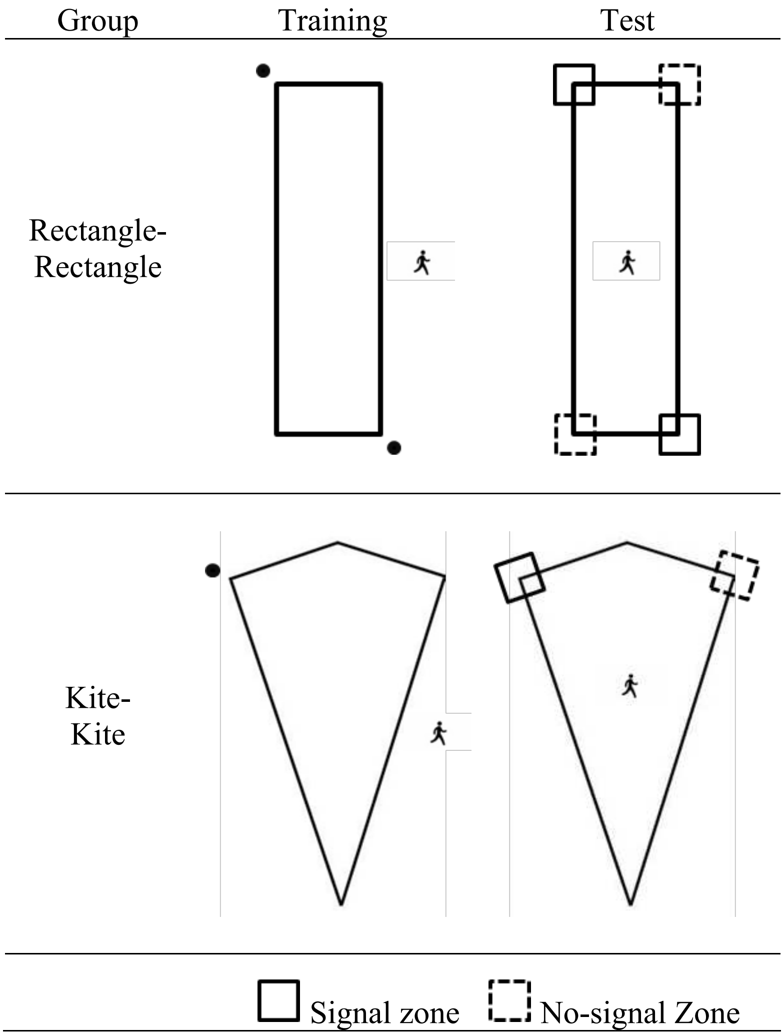


Figure 5.2. Schematic views of the training and test environments for the two groups of Experiment 9b. Black circles represent the location of a hidden goal, and square search zones are superimposed on the diagram of the test environment. The location of the person indicates whether participants were navigating on the inside, or the outside, of the arena.

5.1.1 Method

5.1.1.1 Participants

For Experiment 9a, 32 students were recruited from the University of Nottingham (26 female), aged between 18 and 28 years (mean = 20.78, *SD* = 2.54). For Experiment 9b, a further 32 students, aged between 18 and 41 years (mean = 21.28, *SD* = 4.46), were also recruited from the University of Nottingham (23 female). All participants were given course credit or £5 in return for participation. Participants were randomly allocated to an experimental group, with the stipulation that there were 16 participants in each group.

5.1.1.2 Materials

Mazesuite software (Ayaz et al., 2008; www.mazesuite.com) was used to construct and display the virtual environments that participants, again, viewed from a first-person perspective. These environments were displayed on an Apple Mackintosh model A1224 (EMC2133) with a screen of 274 x 434 mm. The dimensions of the kite- and rectangle-shaped arenas were identical to those reported in Experiment 1. The goals within the arenas were square-shaped regions (1.08m x 1.08m) that were always placed 2.48m away from the walls of the arena, along on a notional line that bisected the corner. When participants were navigating on the inside of the arena, a wooden texture was applied to the floor, and a uniform dark grey texture was applied to the ceiling. The walls of the arena were the cream colour that was reported in Experiment 1. When participants were navigating on the outside of the arena, a grass texture was applied to a 780m x 780m floor, a brick texture was applied to walls of the arena, and the sky was rendered as a uniform black expanse (see Figure 5.3).

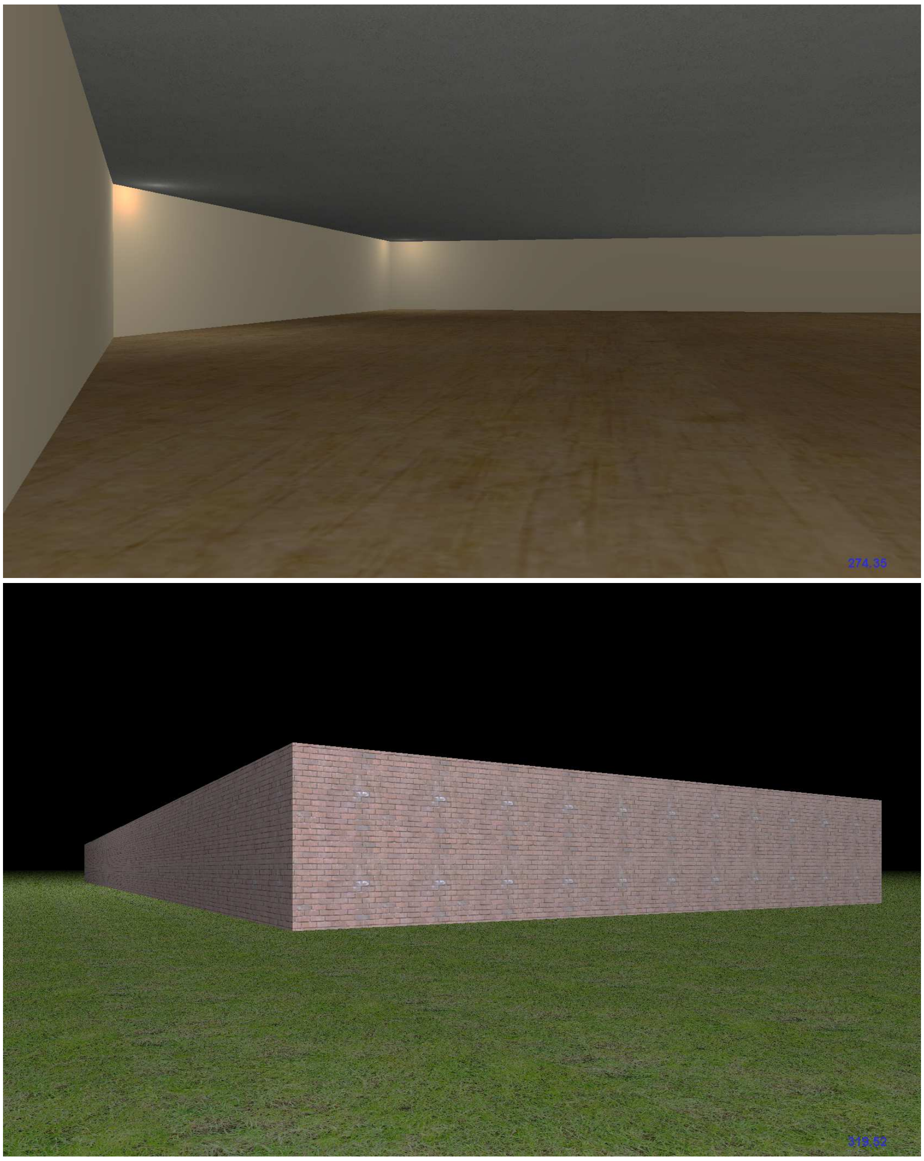


Figure 5.3. Examples of the inside of the kite-shaped arena used in Experiments 9 and 10 (top), and the outside of the rectangle-shaped arena used in Experiments 9, 10, and 11 (bottom).

5.1.1.3 Procedure

After signing a standard consent form, if training was conducted on the inside of an environment, participants were given the following set of instructions on paper.

This study is assessing human navigation using a computer generated virtual environment. During this experiment, you will complete 16 trials. In each trial, you will be placed into a room that contains a Wi-Fi hot spot. Your aim is to end the trials as quickly as possible by walking into the hot spot.

You will view the environment from a first person perspective, and be able to walk into the hot spot from any direction using the cursor keys on the keyboard. Once you've found the hot spot a congratulatory message will be displayed and you should hit enter when you're ready to begin the next trial. You will always be in the centre of the arena when a trial begins, but the direction in which you face at the start of each trial will change.

To start with, you may find the hot spot is difficult to find. The hot spot does not move though, so it is possible to learn its specific location as the experiment goes along. It's a good idea to fully explore the environment on the first few trials to become aware of your surroundings. This should help you in learning where the hidden hot spot is.

This session should take around 20 minutes. If at any point you wish to stop this session, please notify the experimenter and you'll be free to leave without having to give a reason why. Your results will be saved under an anonymous code, and kept confidential throughout.

Minor changes were made to the instructions if participants were trained on the outside of an environment, namely, that participants were searching for a mobile signal hotspot instead of a Wi-Fi hotspot. Participants sat not more than 50 cm from the screen and, for each of the 16 acquisition trials that were administered, participants were required to navigate to the hidden goal by using the cursor keys as described in Experiment 1. As in all previous experiments reported in this thesis, there was no time limit for acquisition trials; thus, each trial ended only when the hidden goal was found. Once the hidden goal had been found, participants could no longer move within the arena and a congratulatory message (For Experiment 9a: *Wi-Fi Connected!* For Experiment 9b: *Signal Found!*) was displayed on screen. Participants pressed enter to begin the next trial.

The 32 participants recruited for Experiment 9a were split, equally, into two groups. Group rectangle-rectangle was trained inside of a rectangle-shaped arena before receiving a test trial conducted on the outside of a rectangle-shaped arena and, likewise, group kite-kite was trained inside a kite-shaped arena before receiving a test trial conducted on the outside of a kite-shaped arena. During training, the location of the hidden goal, for both groups, was counterbalanced such that eight participants within each group were required to navigate to a right-angled corner where a long wall was to the left of a short wall, whilst the remaining eight participants in each group were required to navigate to a right-angled corner where a long wall was to the right of a short wall. As with the kite-shaped arenas, it was desirable to ensure that visits to the correct corner of the rectangle always resulted in finding the hidden goal. As the rectangle-shaped arenas contained two corners which shared the same geometric properties, it was necessary for each rectangle-shaped arena to contain two hidden goals. Experiment 9b was conducted in an identical manner, apart from the fact that participants were trained on the outside of an arena before receiving a test trial conducted on the inside of an arena.

Participants trained inside of an arena travelled at 2m/s during both acquisition and test trials (Mazesuite move parameter set to .005). Those trained inside of a kite-shaped arena began each trial at a point located halfway between the apex and obtuse corners, and the direction in which participants faced at the outset of each trial was randomised for every trial. Participants trained inside a rectangle-shaped arena began each trial at the centre of the environment, again, facing in a random direction for every trial (see Figure 5.4). Participants trained on the outside of these environments were required to traverse greater distances compared to those trained on the inside of an arena when learning the task. In order to not increase the length of time required to complete the task, participants trained on the outside of an arena travelled at 3.6m/s during both acquisition and test trials (Mazesuite move parameter set to .009). Participants trained on the outside of either-shaped arena began each trial facing the centre of one of the four walls (see Figure 5.4), and were located 3.15m away from that wall, along a notional line running perpendicular to the wall. Each of the four walls served as a start location for four acquisition trials for each participant in Experiment 9b. As previously described, in both groups of the experiment, eight participants were required to navigate to a given corner of the arena. Of these eight participants, four received start locations in the order of ADBCDBCABDCACABD, whilst the other four received these start locations in reverse order.

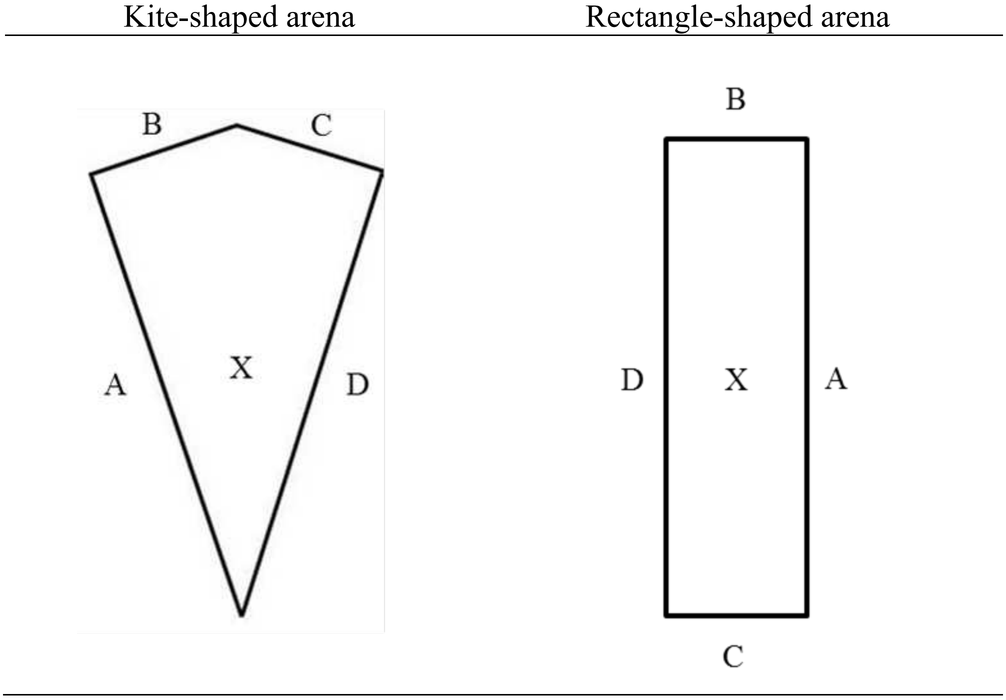


Figure 5.4. Schematic diagrams of the environments used in the experiments. Letter X represents the location in which participants began each acquisition trial when trained to find a hidden goal inside of the environments, during Experiments 9a and 10a. Letters A, B, C, and D represent the locations in which participants began acquisition trials when trained to find a hidden goal on the outside of the environments, during Experiments 9b, 10b, and 11.

Having completed 16 acquisition trials, participants trained inside an arena were presented with the following set of instructions on screen:

In the next trial, you will again have to locate a Wi-Fi signal. The location of the Wi-Fi signal hasn't changed, so it will be in the same location as before.

However, you will be navigating around the outside of the building. As the Wi-Fi signal will be travelling through the walls of the building, it will be a bit weaker, and so it may be harder to locate.

Press enter to start.

If participants were trained on the outside of an arena, they were told the test trial would be conducted on the inside of an arena. For participants in both groups of Experiment 9a, pressing enter began a 120 second test trial in which they were placed on the outside of an arena that contained no hidden goals. Participants began the test trial facing one of the four walls of the shape, and were again located 3.15m from the centre of the wall, along a notional line running perpendicular to the wall. There were 4 possible start locations for the test trial, and each location was used twice in every set of eight participants previously described. For participants in both groups of Experiment 9b, pressing enter began a 60 second test trial in which participants were placed on the inside of an arena that contained no hidden goals. For tests conducted in a kite-shaped arena, participants began each trial at a point located halfway between the apex and obtuse corners and, in a rectangle-shaped arena, they began each trial at the centre of the arena. In both shapes, the direction in which participants began facing was randomised for every trial.

At the beginning of the test trial, it was necessary for participants in Experiments 9a and 9b to establish their orientation using the shape of their environment, before beginning to search for the, now absent, hidden goal. When navigating on the inside of an environment, it is possible to establish orientation based on the shape of the environment by simply rotating to bring each consecutive wall into view. When navigating on the outside of an environment, it is also necessary to view each consecutive wall in order to establish an orientation. This, however, cannot be achieved by simple rotation. Instead, participants must travel in order to bring each wall into view and, consequently, establishing orientation when navigating on the outside of an environment takes considerably longer compared to navigating on the inside of an arena. In order to account for this, and ensure that participants tested on the outside of an environment had sufficient time to search for the absent hidden goal, the test trials conducted on the outside of an arena were 60s longer than those conducted on the inside of an arena.

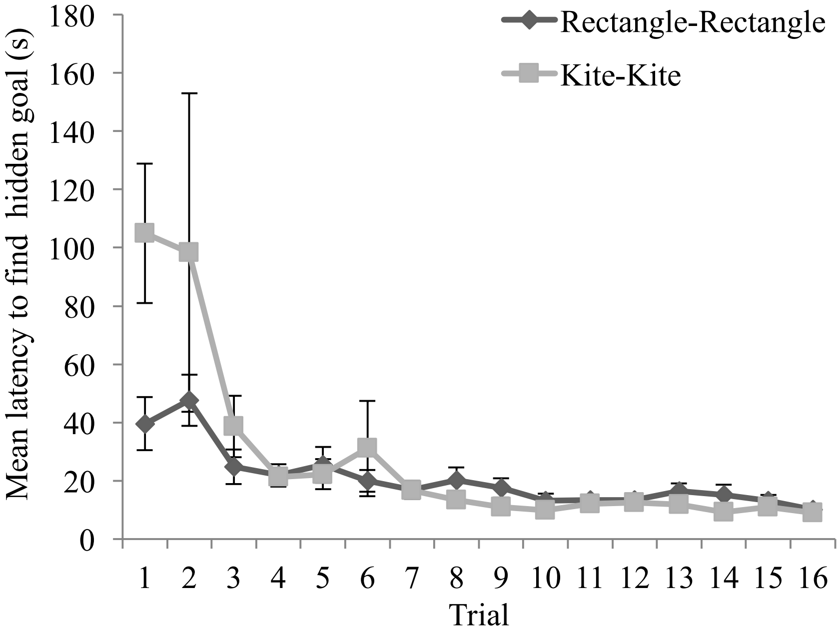
To measure navigational performance during test trials, the time spent within 6.48 x 6.48 m square search zones, which were centred on all points where a long and short wall met to create a right angled corner, was recorded. These search zones were orientated such that two of its edges were parallel to a long wall of an arena, and the remaining two edges ran parallel to a short wall of an arena (see Figure 5.1 and 5.2). Signal zones were defined as the right-angled corners of an environment that had previously contained the hidden goal, and no-signal zones were defined as the other right-angled corners.

5.1.2 Results

5.1.2.1 Experiment 9a

Acquisition (Inside). The top panel of Figure 5.5 shows that the latency, in seconds, from the beginning of each trial to enter the region defined as the hidden goal decreased across trials for both the rectangle-rectangle and kite-kite groups. A two-way ANOVA conducted on individual latencies to find the goal, with a between-subjects factor of group (rectangle-rectangle or kite-kite), and a within-subjects factor of trial (1-16), revealed a significant main effect of trial, *F*(15, 450) = 5.97, *MSE* = 2138.16, $p < .001$, $\eta_p^2 = .17$, confirming that participants found the hidden goal quicker as trials progressed. There was no main effect of group, $F(1, 30) = 2.02$, $MSE = 2708.56$, $p = .17$, $\eta_p^2 = .06$; however, the interaction between group and trial approached significance $F(15, 450) = 1.66$, $MSE = 2138.16$, $p = .056$, $\eta_p^2 = .05$. Simple main effects analysis revealed that this was driven by participants in the rectangle-rectangle group finding the goal quicker on trial 1 compared to participants in the kite-kite group, $F(1, 30) = 6.49$, $MSE = 5267.38$, $p = .016$, $\eta_p^2 = .18$. There were no other differences between groups on any other trials, $F\text{s}(1, 30) < 3.46$, $MSE\text{s} < 24523.34$, $p\text{s} > .073$, $\eta_p^2 < .10$.

Test trial (Outside). The bottom panel of Figure 5.5 displays the time spent, in seconds, searching within the signal and no-signal zones of the arena. Participants in both the rectangle-rectangle and kite-kite groups searched for more time in the signal zone of the arena, compared to the no-signal zone. A two-way ANOVA conducted on individual time spent in zones, with a between-subjects factor of group (rectangle-rectangle or kite-kite), and a within-subjects factor of zone (signal or no-signal), confirmed that participants spent more time in the signal zone, over the no-signal zone $F(1, 30) = 22.93$, $MSE = 227.99$, $p < .001$, $\eta_p^2 = .43$. A significant main effect of group also revealed that participants in the rectangle-rectangle group spent more time in zones compared to participants in the kite-kite group $F(1, 30) = 14.18$, $MSE = 122.79$, $p = .001$, $\eta_p^2 = .32$. There was, however, no significant interaction between group and zone, $F<1$.



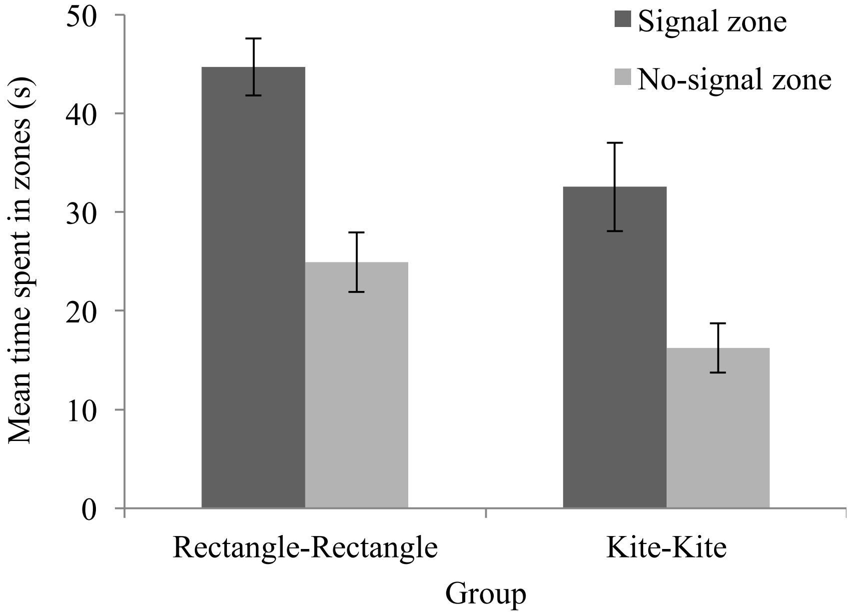
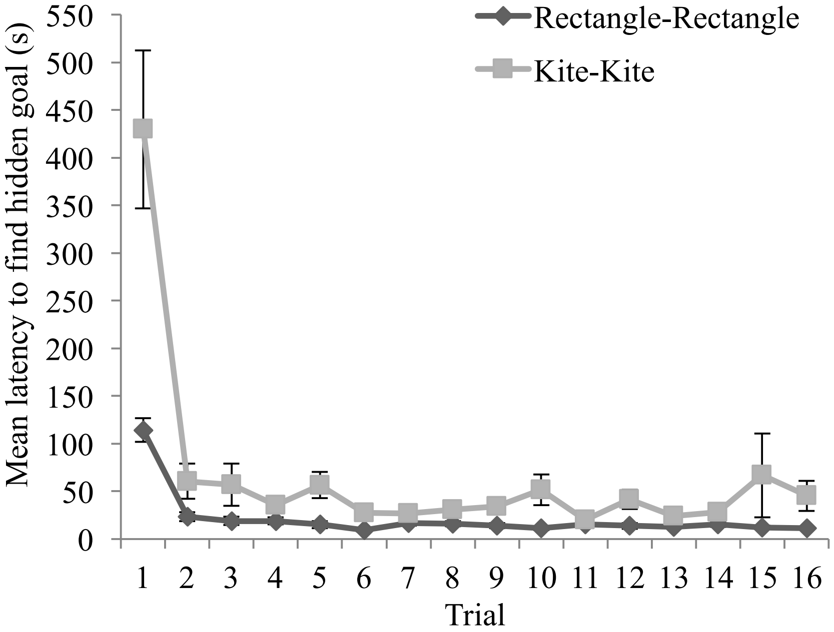


Figure 5.5. Mean latencies to find the hidden goal during acquisition trials (top) and mean time spent in zones during the test trial (bottom) for both group rectangle-rectangle and group kite-kite of Experiment 9a. Error bars show 1 +/- standard error of the mean.

5.1.2.2 Experiment 9b

Acquisition (Outside). The top panel of Figure 5.6 shows the latency, in seconds, from the beginning of each trial to enter the region defined as the hidden goal for both the rectangle-rectangle and kite-kite groups. The latency to find the goal decreased across early trials for both groups, although the rectangle-rectangle group appeared to find the goal quicker than the kite-kite group throughout training. A two-way ANOVA conducted on individual latencies to find the goal, with a between-subjects factor of group (rectangle-rectangle or kite-kite), and a within-subjects factor of trial (1-16), revealed a significant main effect of trial, $F(15, 450) = 21.33$, $MSE = 5684.11$, $p< .001$, $\eta_p^2 = .42$, confirming that participants found the hidden goal quicker as trials progressed. There was also a significant main effect of group, $F(1, 30) = 79.40$, $MSE = 3064.04$, $p< .001$, $\eta_p^2 = .73$, and a significant interaction between group and trial, $F(15, 450) = 7.69$ $MSE = 5684.11$, $p< .001$, $\eta_p^2 = .20$. Simple main effects analysis revealed that participants in the rectangle-rectangle group found the goal quicker than participants in the kite-kite group on trials 1, 5, 6, 8-10, 12, and 16, Fs$(1, 30) > 4.72$, MSEs > 180.16, ps$< .038$, $\eta_p^2 > .14$.

Test trial (Inside). The bottom panel of Figure 5.6 displays the time spent, in seconds, searching within the signal and no-signal zones of the arena. Again, participants in both the rectangle-rectangle and kite-kite groups preferentially searched in the signal zone of the arena, over the no-signal zone. A two-way ANOVA conducted on individual time spent in zones, with a



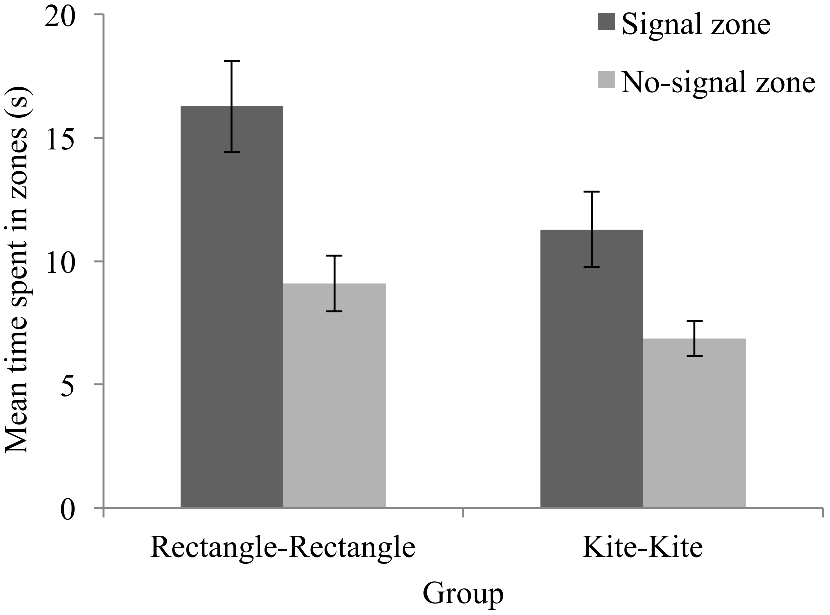


Figure 5.6. Mean latencies to find the hidden goal during acquisition trials (top panel) and mean time spent in zones during the test trial (bottom panel) for both group rectangle-rectangle and group kite-kite of Experiment 9b. Error bars show 1 +/- standard error of the mean.

between-subjects factor of group (rectangle-rectangle or kite-kite) and a within-subjects factor of zone (signal or no-signal), confirmed that participants spent more time in the signal, over the no-signal, zone, $F(1, 30) = 17.16$, $MSE = 31.35$, $p < .001$, $\eta_p^2 = .36$. A significant main effect of group also revealed that participants in the rectangle-rectangle group spent more time in zones compared to participants in the kite-kite group, $F(1, 30) = 7.21$, $MSE = 28.95$, $p = .012$, $\eta_p^2 = .19$. There was, however, no significant interaction between group and zone, $F<1$.

5.1.3 Discussion

In Experiment 9a, participants were trained to find a hidden goal that was located at a distinctive corner inside either a rectangle- or kite-shaped arena. Following this training, participants were placed on the outside of the same shape for a test trial in the absence of the goal. Participants spent more time searching at the outside of the right-angled corner that contained the hidden goal from training compared to the other right-angled corner. The same pattern of results was also observed in Experiment 9b, when participants were first trained to find a hidden goal on the outside of a given shape before receiving a test administered on the inside of the same shape. It is difficult to explain these results from the perspective of a local-shape account of navigation (e.g. Pearce et al., 2004). If, for example, participants learned to navigate to the intersection of a short wall to the left of a long wall during training then, at test, participants should spend more time exploring the corner of the alternative side of the arena that best matches this description. The results of Experiments 9a and 9b clearly demonstrated that this was not the case, as participants spent more time searching next to the corner where the short wall was to the right of the long wall. The current results, therefore, seem to be more consistent with the idea that a global representation of the shape of the environment is acquired during training. For example, if participants in the rectangle-rectangle group from Experiment 1a acquired a representation of the training environment (and the location of the goal within it) in a manner that is comparable to the sketch in the top- left of Figure 5.1, then it is straightforward to understand why participants would explore the top-left and bottom-right corners of the arena when placed on its outside, as these corners are closer to the position where the goal was located than any other external point.

5.2 Experiments 10a and 10b

The purpose of Experiments 10a and 10b was to evaluate the type of global-shape parameter that participants may have used to navigate in Experiments 9a and 9b. In the previous discussion, it was suggested that participants might acquire a relatively rich Euclidian-like representation of the shape of the arena during learning, and refer to this representation at test in order to search for the goal. It is, however, possible that the global encoding is far sparser than this. Cheng and Gallistel (2005) suggested that organisms might encode the principle axis of an arena during navigation, and navigate on the basis of it. The principal axis is colloquially known as the long axis, and passes through the centre of any shape (see Cheng, 2005). In a rectangle, the principal axis connects the centre of each short wall and, in a kite, it runs from the acute corner to the obtuse corner. As noted in Chapter 1, Cheng and

Gallistel (2005) suggested that, during navigation, organisms extract the principal axis of the shape of the environment in which they are navigating, and align a global representation of the Euclidean shapes of environments using this axis. The behaviour of rats in the experiment conducted by Pearce et al. (2004), for example, could then be explained if animals navigated to the corner furthest to the right of the principal axis in both training and test arenas. In both a rectangle- and kite-shaped environment, navigating to the wall furthest to the right of the principal axis would lead the animal to the corners of the training and test arenas which shared the same local geometry.

It is possible that participants in Experiments 9a and 9b learned to navigate to the hidden goal with reference to the principal axis of the arena shape, a strategy that would then permit them to search at the appropriate locations during test, when they were placed on the alternate side of the arena walls. In the present experiment, the global-shape of the arena was changed between training and test from a rectangle to a kite, or vice versa, in order to determine whether participants were navigating on the basis of a sparse (principle axis) or rich (Euclidian) global representation of the shape of the arena in Experiment 1. If participants in Experiment 9a and 9b were navigating on the basis of the Euclidean shape of the environment during test (Cheng, 1986; Gallistel, 1990), then changing the shape of the arena for the test on the alternative side of the arena should remove the preference for searching in one test zone over another, as the remembered shape of the arena would not match the shape of the arena at test. If, however, participants extracted the principal axis of the arena during training in Experiments 9a and 9b, then performance at test would be preserved in the present experiment. In

Experiment 10a, group rectangle-kite were first trained on the inside of a rectangle-shaped arena and then tested on the outside of a kite-shaped arena. Likewise, group kite-rectangle were first trained on the inside of a kite-shaped arena and tested on the outside of a rectangle-shaped arena. The same groups were also used in Experiment 10b; however, participants were trained on the outside of one shape before receiving a test trial inside the other shape.

5.2.1 Method

5.2.1.1 Participants

For Experiment 10a, 32 students were recruited from the University of Nottingham (19 female), aged between 18 and 29 years (mean = 20.34, *SD* = 2.66). For Experiment 10b, a further 32 students, aged between 18 and 33 years (mean = 21.41, *SD* = 3.32), were also recruited from the University of Nottingham (20 female). All participants were given course credit or £5 in return for participation. Participants were randomly allocated to an experimental group, with the stipulation that there were 16 participants in each group.

5.2.1.2 Materials

For Experiment 10a, all materials were identical to Experiment 9a and, similarly, the material details for Experiment 10b were identical to those reported for Experiment 9b.

5.2.1.3 Procedure

Participants in Experiment 10a received identical instructions to those presented in Experiment 9a and, likewise, Participants in Experiment 10b received identical instructions to those presented in Experiment 9b. In group rectangle-kite, participants were trained to find a hidden goal that was always located at a particular corner of a rectangle-shaped environment, before receiving a test trial conducted with a kite-shaped arena. Likewise, group kite-rectangle were trained to find a hidden goal that was always located at a particular corner of a kite-shaped environment, before receiving a test trial conducted with a rectangle-shaped arena. For Experiment 10a, participants were trained inside of an environment and tested outside of an environment (see Figure 5.7). In contrast, for Experiment 10b, participants were trained outside of an environment and tested inside of an environment (see Figure 5.8). In both Experiments 10a and 10b, the training procedure, the test procedure, counterbalancing of the location of the hidden goal, the location in which participants began each trial, and the direction in which they were facing, were all identical to Experiments 9a and 9b, respectively.

To measure navigational performance during test trials, the time spent within 6.48 x 6.48 m square search zones, which were centred on all points where a long and short wall met to create a right angled corner, was recorded. These search zones were, again, orientated such that two of their edges were parallel to a long wall of an arena, and the remaining two edges ran parallel to a short wall of an arena (see Figure 5.7 and 5.8). Signal zones were located at right-angled corners that were the same side of the principal axis as the right-angled corners that contained the hidden goal during training. No-signal zones were located at the other right-angled corners.

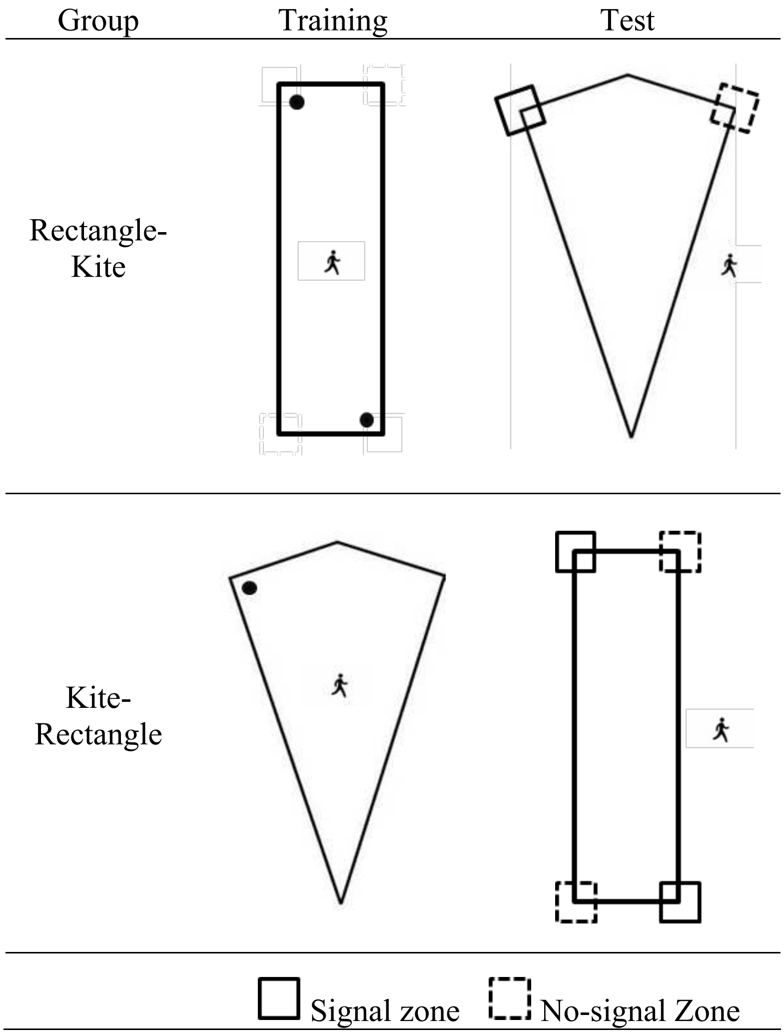


Figure 5.7. Schematic views of the training and test environments for the two groups of Experiment 10a. Black circles represent the location of a hidden goal, and square search zones are superimposed on the diagram of the test environment. The location of the person indicates whether participants were navigating on the inside, or the outside, of the arena.

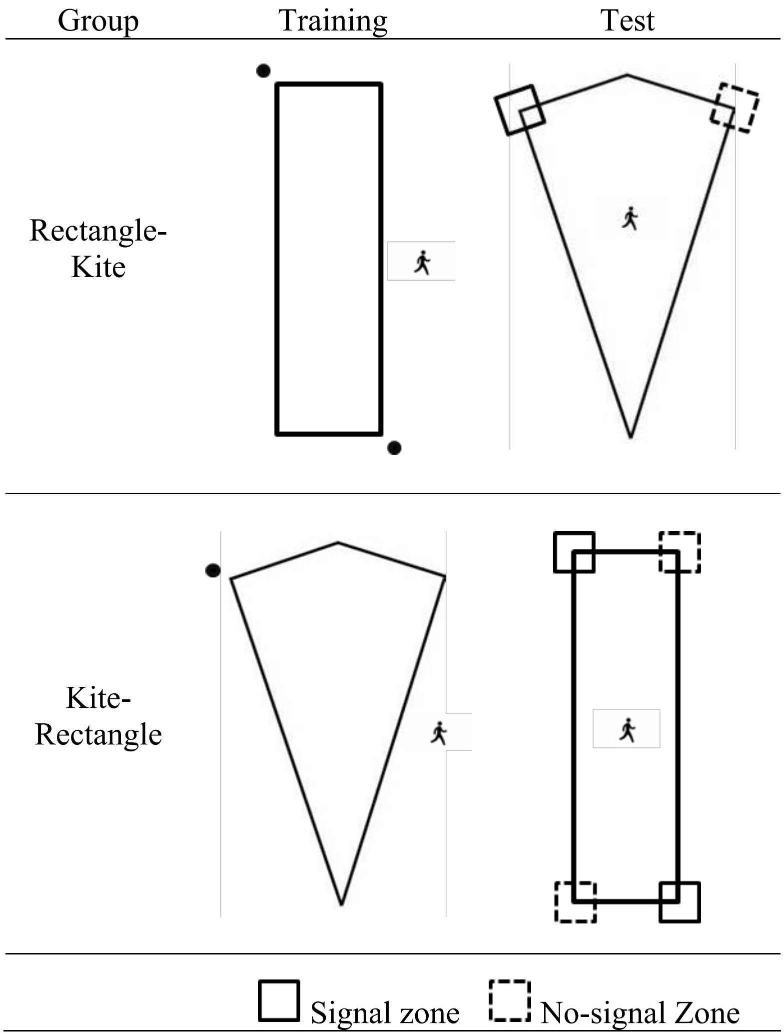


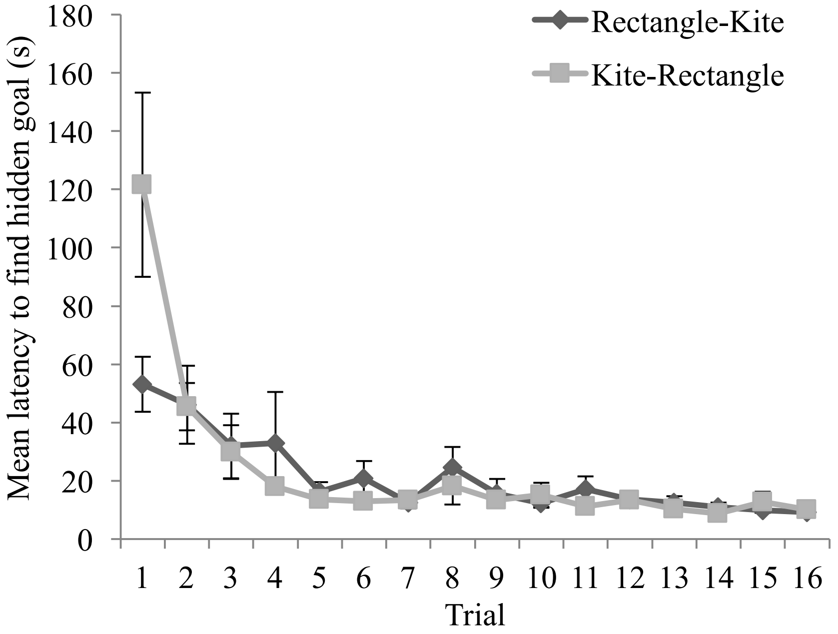
Figure 5.8. Schematic views of the training and test environments for the two groups of Experiment 10b. Black circles represent the location of a hidden goal, and square search zones are superimposed on the diagram of the test environment. The location of the person indicates whether participants were navigating on the inside, or the outside, of the arena.

5.2.2 Results

5.2.2.1 Experiment 10a

Acquisition (Inside). The top panel of Figure 5.9 shows the latency, in seconds, from the beginning of each trial to enter the region defined as the hidden goal for both the rectangle-kite and kite-rectangle groups. The latency to find the goal decreased across early trials for both groups, although the rectangle-kite group appeared to find the goal quicker than the kite-rectangle group on trial 1. A two-way ANOVA conducted on individual latencies to find the goal, with a between-subjects factor of group (rectangle-kite or kite-rectangle), and a within-subjects factor of trial (1-16), confirmed that participants became quicker to find the goal as trials progressed, $F(15, 450) = 12.39$, $MSE = 1011.39$, $p < .001$, $\eta_p^2 = .29$. There was no main effect of group, $F<1$; however, there was a significant interaction between group and trial, $F(15, 450) = 2.66$, $MSE = 1011.39$, $p = .001$, $\eta_p^2 = .08$. Simple main effects analysis revealed that participants in the rectangle-kite group found the goal quicker than participants in the kite-rectangle group on trial 1 only, $F(1, 30) = 4.31$, $MSE\text{s} = 8699.87$, $p = .047$, $\eta_p^2 = .13$.

Test trial (Outside). The bottom panel of Figure 5.9 displays the time spent, in seconds, searching within the signal and no-signal zones of the arena. Participants, in both the rectangle-kite and kite-rectangle groups, spent a similar amount of time searching in both zones during the test trial. A two-way ANOVA conducted on individual time spent in zones, with a between-subjects factor of group (rectangle-kite or kite-rectangle), and a within-subjects factor of zone (signal or no-signal), revealed only a significant main effect of group,



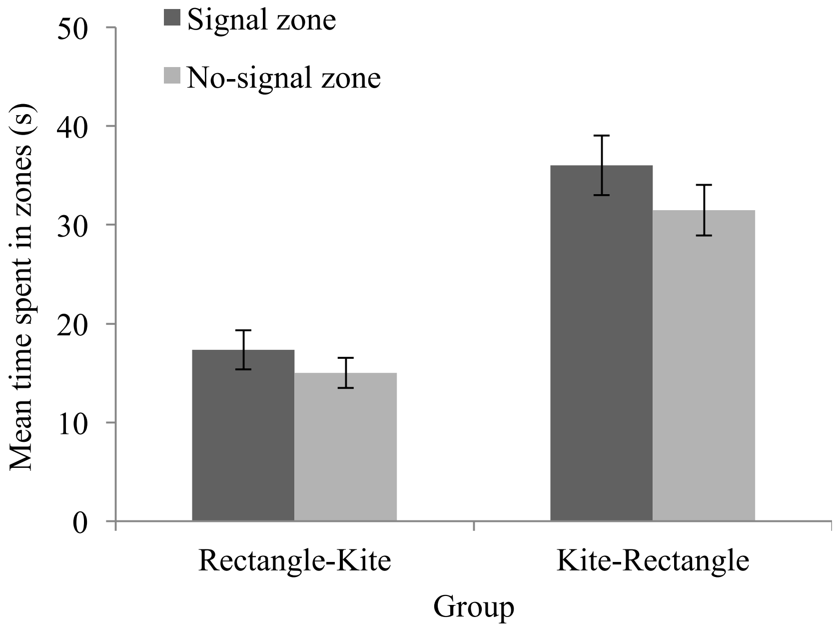


Figure 5.9. Mean latencies to find the hidden goal during acquisition trials (top) and mean time spent in zones during the test trial (bottom) for both group rectangle-kite and group kite-rectangle of Experiment 10a. Error bars show 1 +/- standard error of the mean.

$F(1, 30) = 83.59$, $MSE = 59.20$, $p<.001$, $\eta_p^2 = .74$, with participants in the kite-rectangle group spending more time in zones than participants in the rectangle-kite group. The main effect of zone was not significant, $F(1, 30) = 1.61$, $MSE = 118.20$, $p=.21$, $\eta_p^2 = .05$, nor was the interaction between zone and group $F<1$.

5.2.2.2 Experiment 10b

Acquisition (Outside). The top panel of Figure 5.10 shows the latency, in seconds, from the beginning of each trial to enter the region defined as the hidden goal for both the rectangle-kite and kite-rectangle groups. The latency to find the goal decreased across early trials for both groups, although participants trained with a rectangle-shaped arena (group rectangle-kite) appeared to find the goal quicker than participants trained with a kite-shaped arena (group kite-rectangle) throughout training. A two-way ANOVA conducted on individual latencies to find the goal, with a between-subjects factor of group (rectangle-kite or kite-rectangle), and a within-subjects factor of trial (1-16), revealed a significant main effect of trial $F(15, 450) = 14.51$, $MSE = 1218.06$, $p< .001$, $\eta_p^2 = .33$, confirming that participants became quicker to find the goal as trials progressed. There was also a main effect of group $F(1, 30) = 12.06$, $MSE = 4955.94$, $p< .001$, $\eta_p^2 = .29$, confirming that the rectangle-kite group took less time, overall, to find the hidden goal relative to the kite-rectangle group. The interaction between group and trial was not significant $F(15, 450) = 1.48$, $MSE = 1218.06$, $p= .11$, $\eta_p^2 = .047$.

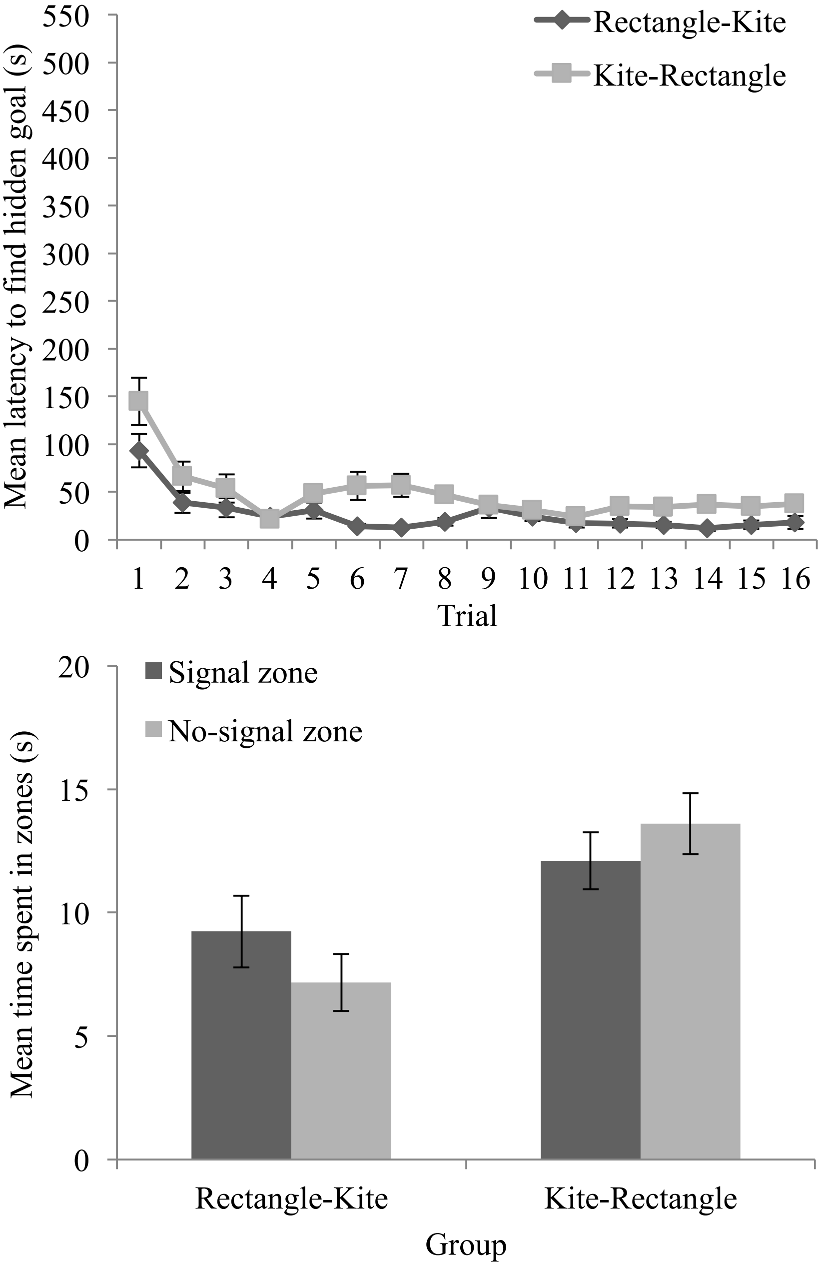


Figure 5.10. Mean latencies to find the hidden goal during acquisition trials (top) and mean time spent in zones during the test trial (bottom) for both group rectangle-kite and group kite-rectangle of Experiment 10b. Error bars show 1 +/- standard error of the mean.

Test trial (inside). The bottom panel of Figure 5.10 displays the time spent, in seconds, searching within the signal or no-signal zones of the arena. Again, participants in both the rectangle-kite and kite-rectangle groups spent an equivalent amount of time searching in both types of zone during the test trial. A two-way ANOVA conducted on individual time spent in zones, with a between-subjects factor of group (rectangle-kite or kite-rectangle), and a within-subjects factor of zone (signal or no-signal), again revealed only a significant main effect of group, $F(1, 30) = 10.44$, $MSE = 33.06$, $p = .003$, $\eta_p^2 = .26$. Participants in the kite-rectangle group spent more time in any of the measured zones compared to participants in the rectangle-kite group. The main effect of zone was not significant, $F<1$, nor was the interaction between zone and group $F(1, 30) = 2.89$, $MSE = 17.40$, $p = .10$, $\eta_p^2 = .09$.

5.2.3 Discussion

Following a change in shape between training and testing environments, participants in Experiments 10a and 10b displayed no preference for searching in any of the right-angled corners of the test environment when moved from one side of the arena to the other (e.g. from inside to outside). These results are inconsistent with the idea that organisms extract the principal axis of the shapes of the environments they navigate in, and guide navigation using this parameter (Cheng & Gallistel, 2005). If participants in Experiments 10a and 10b were navigating on the basis of the principal axis then, as in Experiments 9a and 9b, a preference for searching in the signal zone, over the no-signal zone, should have been observed at test. The results of Experiments 10a and 10b are, however, consistent with the predictions made from the account that participants navigated on the basis of a global representation of only the Euclidean geometry of the environments. Making a full change in the shape of the arena between training and test will result in the global representations of these two shapes failing to match, resulting in a loss of the preference for searching in one test zone over another. Like Experiments 9a and 9b, the results of Experiments 10a and 10b also provide no support for the idea that participants navigated using a representation of local-shape information at test. If participants learned, in stage 1, to find the goal inside the corner of a rectangle where the long wall was to the left of a short wall then, when transferred to the outside of a kite-shaped arena, participants should have explored the corner of the exterior of the arena that best matched this local corner and approached the exterior corner where the long wall was to the left of a short wall. They did not.

An additional benefit of conducting Experiments 10a and 10b was that it rules out the possibility that, in Experiments 9a and 9b, participants were using some form of mental rotational strategy to solve the task, such as a perspective transformation (Tversky, Kim, & Cohen, 1999; Zacks, Vettel, & Michelon, 2003). That is, during training, participants may have encoded only the local-shape information that signalled the goal location and, during the test trial, imagined what this local information would look like from a different perspective. For example, a participant who learned that, on the inside of the arena, the goal was located in a right angled corner where a short wall is to the left of a long wall could then transform this representation in order to search where a short wall to the right of a long wall creates a 270° degree join, on the outside of the environment. If participants were using such a strategy in

Experiments 9a and 9b, and the Euclidean shape of the environments did not contribute to their search preference, then it stands to reason that participants in Experiments 10a and 10b should display the same search preference as participants in Experiments 9a and 9b. This, however, was not the case.

Participants in Experiments 10a and 10b did not show a significant preference for searching in the corners that would be predicted by navigation based on the principal axis or local-shape information of the test environment. It is important, however, to determine whether this non-significant result supports the null hypothesis (that there was no difference in time spent in each zone), or no conclusion at all (Dienes, 2011). To determine between these possibilities a Bayes factor was calculated, where values less than .33 indicate support for the null hypothesis, values above 3 indicate support for the alternative hypothesis, and values between .33 and 3 indicate no support for either hypothesis (Jefferys, 1961; see Dienes, 2008 for a rationale). To calculate a Bayes factor, it is necessary to estimate a plausible effect size. In order to achieve this, the data from Experiments 9a and 9b were combined, and collapsed across groups. Using the data from all 64 participants recruited from Experiment 9, there was a mean difference of 11.94s between the duration of time spent in the signal and no-signal zones. Combining data from Experiments 10a and 10b and collapsing across groups, a mean difference of 1.87s (*SE* = 1.45) was observed. Following Dienes (2011: see also www.lifesci.sussex.ac.uk/home/Zoltan_Dienes/inference/Bayes.htm), Experiments 10a and 10b were modelled with a 2-tailed distribution with a mean of 0 (indicating no difference between the time spent in the signal and no-signal zone) and a *SD* set to 11.94. This yielded a Bayes factor of .27, indicating support for the null hypothesis.

There are two possible reasons why participants spent an equal amount of time in both zones during the test trials of Experiment 10. First, it might be argued that participants displayed an equal preference for both zones because of conflicting information provided by both the principal axis and local-shape information – a possibility that will be returned to in the general discussion to this chapter. Second, for some reason, participants may simply not have been able to guide their navigational behaviour on the basis of either (i) the local-shape information, or (ii) the principal axis of environments, when navigating on the outside of the environments. This latter suggestion draws into question the logic of the experiments that have been presented so far in this chapter. Experiment 11 was conducted in order to determine whether participants could use the principal axis of an environment, or local-shape information, to guide navigation on the outside of an environment.

5.3 Experiment 11

A number of experiments have now shown that when training and testing both occur inside arenas, participants will display a bias in search behaviour, despite a change in the global-shape of the environment. In Experiment 1, for example, participants trained to find a goal hidden at the inside corner of a rectangle where a long wall is to the left of a short wall preferentially searched for the goal at the corner of a kite-shaped arena that has the same local-shape cues (see also: Esber et al., 2005, Lew et al., 2014; Lubyk et al., 2012; McGregor et al., 2006; Pearce et al., 2004; Poulter et al., 2013; Tommasi & Polli, 2004). In terms of the outcomes of Experiments 10a and 10b, these results are reassuring, as they point to the fact that spatial navigation can transfer between arenas that have different overall shapes on the basis of either local-shape information, or the principal axis of the environments. Consequently, the disruption of navigation that was observed in Experiments 10a and 10b may not have been a consequence of the change in the global-shape of the arena *alone* but, instead, a consequence of a change of global-shape *in conjunction with* a shift from the inside to the outside of the arena (or vice versa). All of the experiments that have tested transfer of search behaviour between arenas of different overall shapes have, however, been conducted with training and testing conducted on the inside of these arenas. It is, therefore, possible that the same transfer would not be evident if training and testing occurred on the outside of the arena. This being the case would hinder the interpretation of Experiments 10a and 10b, as a failure to observe transfer between one side of the arena to the other might solely be due to the fact that training (or testing) occurred on the outside of the arena which might not support spatial transfer between different overall shapes.

Experiment 11 sought to replicate the effects observed in Experiment 1 when administering training and testing outside of a shape, to ensure the suitability of the testing procedure. Participants in group rectangle-kite were trained to find a hidden goal on the outside of a rectangle-shaped arena before receiving a test trial administered on the outside of kite-shaped environment. Similarly, participants in group kite-rectangle were trained on the outside of a kite-shaped arena and tested on the outside of a rectangle-shaped arena (see Figure 5.11).

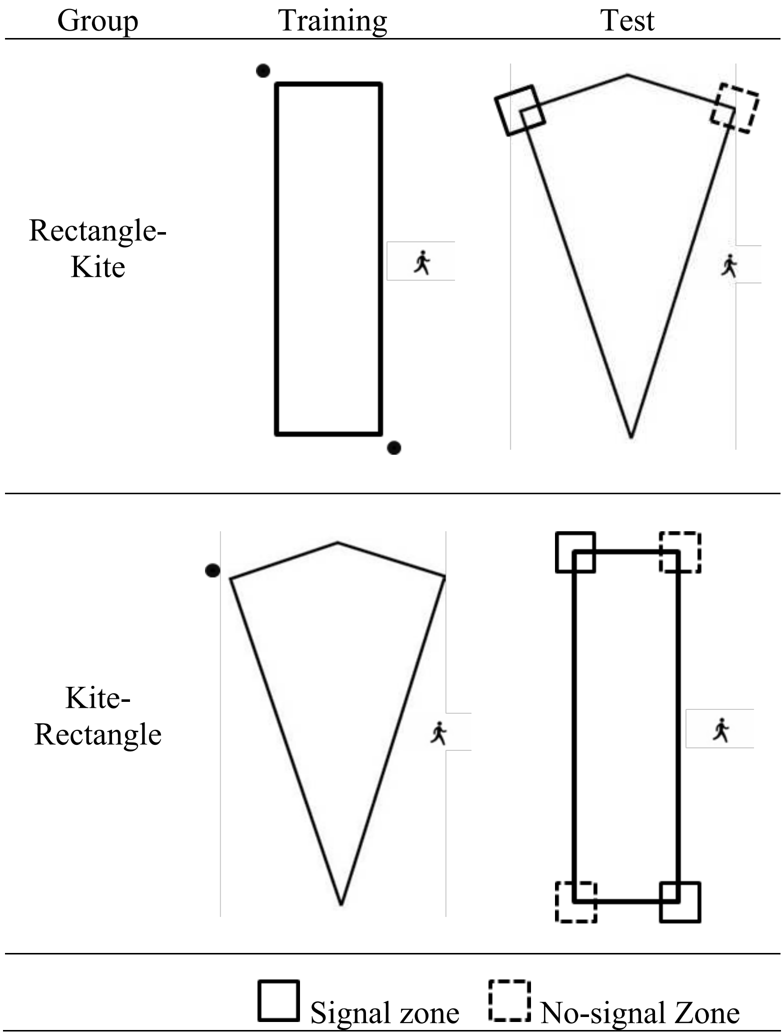


Figure 5.11. Schematic views of the training and test environments for the two groups of Experiment 11. Black circles represent the location of a hidden goal, and square search zones are superimposed on the diagram of the test environment. The location of the person indicates that participants were navigating on the outside of all arenas.

Based on the results of the experiments presented in Chapter 2, and previous studies (Lew et al., 2013; Lubyk et al., 2012; McGregor et al., 2006; Pearce et al., 2004; Poulter et al., 2013; Tommasi & Polli, 2004), it was expected that participants would successfully transfer their search behaviour from the training stage to the test stage, despite the transformation of the testing arena to a different shape. For example, participants trained to find the hidden goal adjacent to the exterior corner of a rectangle-shaped arena where the long wall was to the left of a short wall would search at the corner that shared these same local-shape cues when tested on the outside of a kite-shaped arena.

5.3.1 Method

5.3.1.1 Participants

32 undergraduates were recruited from the University of Nottingham (23 female), aged between 18 and 37 years (mean = 21.66, *SD* = 5.19). All participants were given course credit or £5 in return for participation. Participants were randomly allocated to an experimental group, with the stipulation that there were 16 participants in each group.

5.3.1.2 Materials

All material details for training arenas were identical to those presented for Experiment 9b. All testing arenas were identical to those presented for Experiment 9a.

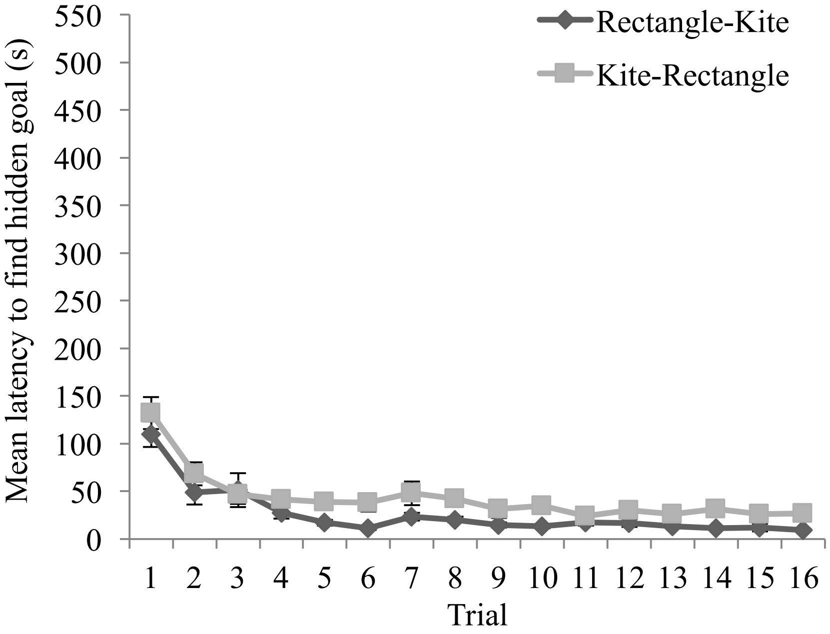
5.3.1.3 Procedure

Participants in group rectangle-kite were trained to find a hidden goal at a particular corner of a rectangle-shaped environment, before receiving a test trial on the outside of a kite-shaped arena. In contrast, participants in group kite-rectangle were trained to find a hidden goal at a particular corner of a kite-shaped environment, before receiving a test trial on the outside of a rectangle-shaped arena. For both groups, the training procedure was identical to Experiments 9b and 10b, and the testing procedure was identical to Experiments 9a and 10a. The signal and no-signal zones used to record behaviour during the test trial were defined in same manner as described for Experiment 10.

5.3.2 Results

5.3.2.1 Acquisition (outside)

The top panel of Figure 5.12 shows that the latency, in seconds, from the beginning of each trial to enter the region defined as the hidden goal decreased across trials for both the rectangle-kite and kite-rectangle groups. Participants navigating outside of a rectangle-shaped arena (group rectangle-kite) found the goal quicker than participants navigating on the outside of a kite-shaped arena (group kite-rectangle) throughout training. A two-way ANOVA conducted on individual latencies to find the goal, with a between-subjects factor of group (rectangle-kite or kite-rectangle), and a within-subjects factor of trial (1-16), revealed a significant main effect of trial, $F(15, 450) = 22.01$, $MSE = 958.02$, $p < .001$, $\eta_p^2 = .42$, confirming that participants became quicker to find the goal as trials progressed. There was also a main effect of group, $F(1, 30) = 19.24$, $MSE = 1867.34$, $p < .001$, $\eta_p^2 = .39$, confirming that the rectangle-kite group took less time to find the hidden goal relative to the kite-rectangle group during the course of training. The interaction between group and trial was not significant, $F<1$.



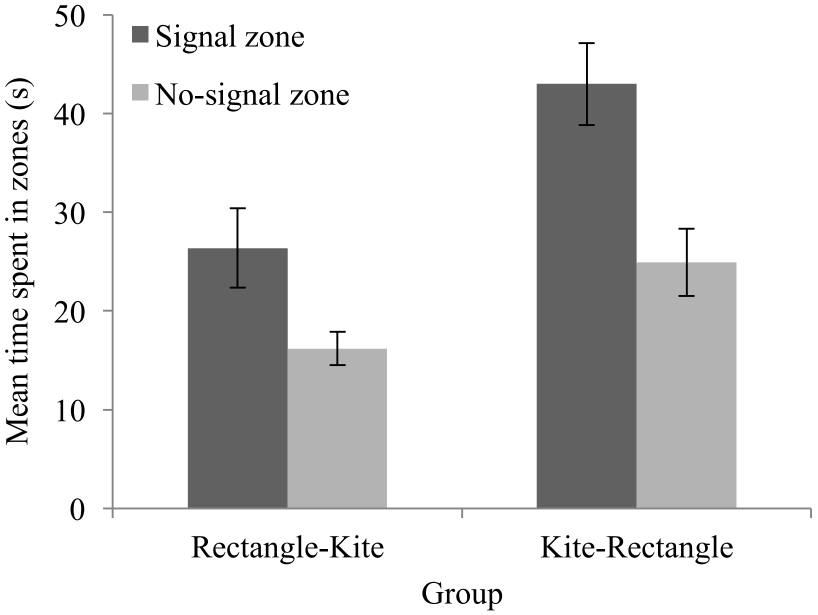


Figure 5.12. Mean latencies to find the hidden goal during acquisition trials (top) and mean time spent in zones during the test trial (bottom) for both group rectangle-kite and group kite-rectangle of Experiment 11. Error bars show 1 +/- standard error of the mean.

5.3.2.2 Test trial (outside)

The bottom panel of Figure 5.12 shows the time spent, in seconds, searching within the signal and no-signal zones of the arena. Participants in both the rectangle-kite and kite-rectangle groups searched for more time in the signal zone of the arena, compared to the no-signal zone. A two-way ANOVA conducted on individual time spent in zones, with a between-subjects factor of group (rectangle-kite or kite-rectangle), and a within-subjects factor of zone (signal or no-signal), revealed a main effect of zone, $F(1, 30) = 12.54$, $MSE = 254.60$, $p< .001$, $\eta_p^2 = .29$, confirming that participants spent more time in the signal zone than the no-signal zone. A significant main effect of group also revealed that participants in the kite-rectangle group spent more time in both zones compared to participants in the rectangle-kite group, $F(1, 30) = 20.52$, $MSE = 125.22$, $p= .001$, $\eta_p^2 = .41$. There was, however, no significant interaction between group and zone, $F<1$.

5.3.3 Discussion

Participants trained to find a hidden goal at a corner on the outside of an arena that had a distinctive shape preferentially searched at the same exterior corners of a different-shaped environment that shared the same local-shape cues. These data replicate, and extend the generality of, the results of a number of previous studies in which training and testing has occurred on the inside of an environment (Esber et al., 2005, Lew et al., 2014; Lubyk et al., 2012; McGregor et al., 2006; Pearce et al., 2004; Poulter et al., 2013; Tommasi & Polli, 2004). More importantly, for the current discussion, they demonstrate that it seems not to matter whether the shape of the arena changes from a rectangle to a kite between training and test when both of these stages of the experiment are conducted on the same side (inside *or* outside). Experiment 11 (along with Experiments 9a and 9b), therefore, serves as a positive control for Experiments 10a and 10b. In section 5.4, these results will permit more substantive discussion about the mechanisms that might underpin the transfer of search behaviour between the inside and the outside of an arena, when its overall shape remains the same, or changes.

5.4 General Discussion

In Experiments 9a and 9b, participants were trained to find a hidden goal in the right-angled corner of one side of an arena (e.g. an inside corner of a kite). At test participants were placed on the alternate side of the same shape (e.g. the outside of the kite). In both Experiments 9a and 9b, participants spent more time exploring the right-angled corner, at test, that would have been closest to the goal signal during training. In Experiments 10a and 10b, participants were again trained to find a hidden goal on one side of an arena, before receiving a test on the alternate side of the arena. For Experiments 10a and 10b, however, the Euclidean shape of the training arena was changed from a kite to a rectangle (or vice versa) between training and test. Under these circumstances, participants displayed no preference for searching by either of the right-angled corners at test. Finally, Experiment 11 revealed that a change in only the shape of the arena between training and testing was not sufficient to disrupt transfer of navigation. Participants were trained to find a goal hidden by an exterior right-angled corner of one shape (e.g. a kite). At test, the global-shape of the arena was changed (e.g. to a rectangle) and, despite this change, participants preferentially searched by the right-angled corner that shared the same local-shape cues on the outside of a rectangle as the kite.

Prior to discussing the theoretically interesting implications of the data reported in this chapter, it is important to address two findings that have been observed in Experiments 9, 10, and 11. First, participants trained with a rectangle-shaped arena found the goal quicker than participants trained with a kite-shaped arena. Second, participants tested in rectangle-shaped arenas spent more time in any of the measured zones compared to participants tested in kite-shaped arenas. As with Experiments 1, 2 and 3, both of these effects can be explained by the fact the rectangle-shaped arenas in Experiments 9, 10, and 11 contained twice as many hidden goals, or twice as many measured zones, compared to the kite-shaped arenas. Consequently, during training, participants trained in a rectangle-shaped arena had a 50% chance of navigating to a corner that contained a hidden goal, whereas, participants trained in a kite-shaped arena only had a 25% chance. Similarly, the total time spent in any of the measured zones during a test trial conducted with a rectangle-shaped environment was the sum of four zones whereas, for a test trial conducted with a kite-shaped environment, it was only the sum of two zones.

Turning now to the results of the test trials, it is difficult to explain the results from Experiments 9, 10, and 11 by assuming that organisms encode only one representation of the space they navigate in, as the results of at least one of these experiments are inconsistent with theories of navigation based on local-shape information, a global representation of the Euclidian shape of the environment, or the principal axis of an environment. First, if animals encoded only local-shape information (e.g. Pearce et al., 2004) then it would be possible to account for the results of Experiment 11 by suggesting that participants navigated on the basis of the local-shape cues that signalled the location of the hidden goal during training, and transferred this behaviour to the novel test environment. It is, however, difficult to then explain why participants displayed no preference for searching in the corner consistent with navigation based on local-shape cues during Experiments 10a and 10b. In Experiments 9a and 9b, moreover, participants failed to search by the corner that best matched the local properties of the corner from training (non-signal zone) and, instead, searched more at the alternative corner (signal zone).

Second, the notion that animals only encode a representation of the Euclidean geometry of the environment (Cheng, 1986; Gallistel, 1990) is consistent with the observation that participants preferentially searched in the signal zone during the test trials of Experiments 9a and 9b. Navigating on the basis of only a representation of the Euclidean shape of an environment is also consistent with the fact that participants displayed no preference for any corner during the test trials of Experiments 10a and 10b, as the global geometry of the training and testing environments differed. Navigation based on the Euclidean geometry of the environment is not, however, consistent with the results of Experiment 11. As with Experiments 10a and 10b, the overall shape of the training and test environments differed in Experiment 11, and so participants should have displayed no preference for any corner. Instead, participants preferentially searched in the corner predicted by theories of navigation based on local-shape cues and the principal axes of shapes (see also: Experiment 1;

Esber et al., 2005, Lew et al., 2014; McGregor et al., 2006; Pearce et al., 2004; Poulter et al., 2012; Tommasi & Polli, 2004).

Third, navigation based solely on the principal axis of the geometry of the environment (Cheng & Gallistel, 2005) can account for the results of Experiments 9a, 9b and 11. At test, in all these experiments, participants searched on the same side of the principal axis that they were trained to navigate to during stage 1. If, though, participants in Experiment 11 transferred navigational behaviour between kite- and rectangle-shaped environments (and vice versa) only on the basis of the principal axis, then it is difficult to explain why a similar preference for the signal zone was not observed in Experiments 10a and 10b.

Given the above discussion, it seems necessary to invoke multiple representations of environmental shape in order to successfully explain the data reported in this chapter. One way to explain the observations reported here is to assume that participants encoded the location of the goal with respect to an allocentric representation (view-independent) of the Euclidean shape of the arena, as well as with respect to an egocentric representation (view-dependent) of the local-shape information at the goal corner. Between the training and test trials of Experiments 9 and 10, participants experienced an unexpected change in view-point (i.e. a move from inside to outside, or vice versa), and it has been argued that behaviour based on egocentric representations is disrupted following such a change in reference point (e.g. Burgess, 2006, 2008). Search behaviour at test in these experiments, therefore, would have been determined only by the allocentric representation of the

Euclidean shape of the arena. This would permit a search bias to emerge in Experiments 9a and 9b, but not in Experiments 10a and 10b, as the overall shape of the training and test environments were only congruent in Experiments 9a and 9b. The overall shape of the training and test environments were not congruent in Experiment 11, however, in this experiment there was not an unexpected change in reference point between training and test. Consequently, transferring local-shape information from the training to the test environment would permit a search bias to occur. The results of Experiment 11, then, would be considered formally equivalent to those presented by Pearce et al. (2004).

Whilst it is possible to explain the results of Experiments 9, 10, and 11 by assuming that participants navigated on the basis of an allocentric representation of the Euclidean shape of the environment, and an egocentric representation of local-shape information, it is not possible to rule out the suggestion that participants also encoded the principal axes of the shapes they navigated within. It is possible to account for the results of the three experiments reported in this chapter by assuming that search behaviour at test is a function of the integration of different search biases established from different representations. Participants in Experiment 9, therefore, preferentially searched at the signal corner because this was consistent with navigation on the basis of a representation of the Euclidean shape of the environment, and with the principal axis of the shape, whereas searching at the non-signal corner was only consistent with navigation based on local-shape information. In Experiment 10, participants did not display a search bias because searching at the signal corner was consistent with navigating on the basis of the principal axis of the shape, and searching at the no-signal corner was consistent with navigation based on local-shape information. Finally, participants preferentially searched in the signal corner in Experiment 11 because this was consistent with navigation based on the principal axis and local-shape information, and searching at the no-signal corner was not consistent with any spatial representation. One manner in which search biases established from different representations of environmental shape may be integrated is by a weighting system that determines what representations are used to guide navigational behaviour on the basis on the current task (Ratliff & Newcombe, 2008; See also Cheng & Newcombe, 2005; Cheng, Shettleworth, Huttenlocher, & Rieser, 2007; Nardini, Jones, Bedford, & Braddick, 2008; Twyman & Newcombe, 2010), and the argument above is predicated on the assumption that representation is given an equal weighting. As noted in a recent review by Cheng, Huttenlocher, and Newcombe (2013), though, it is necessary to precisely specify how search biases, that are established from such radically different spatial representations, would combine to determine navigation behaviour under this weighting approach.

It is worth highlighting that, in order to explain the data observed in Experiments 9-11, it appears necessary to assume that organisms encode a Euclidean representation of the shape of the environment in which they navigate. This finding is consistent with the findings of Experiment 6, in which participants recognised the global-shape of the environments in which they had previously navigated, even when the shape of the environment was not task relevant. One possible to contention to this point is that, in a manner consistent with previous literature (e.g. Cheng & Gallistel; Pearce et al., 2004;

McGregor et al., 2006), it has been assumed that local shape-information is encoded in an egocentric framework. It could, however, be suggested that local shape-information is encoded in an allocentric manner, and there is little evidence to argue against this notion. If local-shape information is encoded in an allocentric manner, it is possible to account for the results of Experiment 9 and 11 by assuming that participants navigated to the exterior corner that matched the allocentric representation that was encoded during training. It is, however, somewhat difficult to explain the results of Experiment 10. For instance, if local shape-information is encoded in an allocentric manner, then participants trained on the inside of a rectangle-shaped arena would be expected to display a preference for an exterior corner of a kite-shaped arena, as was observed in Experiment 11. In order to explain the reduced preference for the signal zone in Experiment 10, relative to Experiment 11, it would have to be assumed that there was greater generalisation decrement when a change in shape between training and test was accompanied by a shift from one side of the arena to another (Experiment 10), compared to when this shift in viewpoint did not occur (Experiment 11). If this argument is accepted, then the experiments presented in this chapter provide evidence that shape-information is encoded in an allocentric manner, but are not able speak to whether this information is local or global in nature.

5.4.1 Conclusion

The notion that organisms encode a Euclidean representation of the shape of their environment was suggested some 25 years ago (Cheng 1986; Gallistel, 1990) and, despite a lack of evidence to support this claim, it continues to be influential in the spatial learning literature. Our knowledge about the manner in which organisms learn about boundaries, however, has been based largely on studies that have examined navigation within environments. There has been little focus on the study of how organisms navigate around bounded environments, or transfer their search behaviour between one side of an environment to the other (e.g. from the inside to the outside of a building). This has been an important omission for two reasons. First, humans regularly navigate around the boundaries of large environments in order to find a goal (such as when attempting to find the appropriate entrance to a sports stadium) and also transfer their search behaviour across environmental boundaries (such as when trying to locate a hole on the inside of a building having drilled into it from the outside). Second, theories of shape-based navigation (e.g. Cheng, 1986; Cheng & Gallistel, 2005; Gallistel, 1990; Miller & Shettleworth; 2007, 2008, 2013; Pearce, 2009) are limited by experiments conducted only in the context of participants navigating within a bounded space. By studying navigation on the outside of a bounded space, the results presented in this chapter provide core evidence that adult humans navigate using a representation of the Euclidean geometry of the environments. An important challenge for future research will be to determine the precise conditions under which this representation of the Euclidean geometry combines with other spatial representations to control navigational behaviour, as well as interfere with it.

Chapter 6

General discussion

In Experiment 1, participants who were trained to locate a hidden goal in one corner of a rectangle-shaped arena subsequently expressed a bias towards searching in a corner of the same local geometry in a kite-shaped arena (and vice versa). In Experiment 2, participants were, first, trained to find hidden goal with respect to non-geometric wall colours of a square-shaped arena. In a subsequent stage, participants were placed into a rectangle-shaped arena that was built from the same coloured walls and, again, had to locate a hidden goal. Finally, participants were given extinction tests in a kite-shaped arena that contained the same local geometric cues as the rectangle-shaped arena; however, the walls of the kite were the same colour. When the same wall colours signalled the goal location in stage 1 and stage 2 of the experiment, participants displayed no search bias in the kite-shaped arena. In contrast, if the wall colours that signalled the goal location in stage 1 and stage 2 differed, participants searched in the corner of the kite-shaped environment that shared the same local geometry as the corner that signalled the goal location in the rectangle-shaped environment. In stage 1 of Experiment 3, participants were required to find a hidden goal in a rectangle-shaped environment, the walls of which were the same colour. In stage 2, participants were placed into a kite-shaped environment that comprised differently-coloured walls. Finally, participants received a test trial, conducted in extinction, in a square-shaped arena built from the same-coloured walls as the kite-shaped arena. Like Experiment 2, when the same local geometric cues signalled the goal location in stage 1 and stage 2 of the experiment, participants displayed no search bias in the square-shaped arena. When different local geometric cues signalled the goal location, however, participants preferentially searched in the corner of the square environment that shared the same wall colours as the corner of the kite-shaped arena that signalled the goal location in stage 2.

In Experiment 1, navigation that was based upon an environment's geometry survived a transformation of its overall shape, a finding that is inconsistent with proposals that organisms navigate using only a global representation of the shape of the environment (e.g. Cheng, 1986; Gallistel, 1990). This finding is, however, consistent with the notion that animals navigate on the basis of local geometric information (e.g. McGregor et al., 2006; Pearce et al., 2006). The results of Experiments 2 and 3 are, moreover, consistent with the associative analysis of spatial learning proposed by Miller and Shettleworth (2007, 2008, 2013). Learning about local geometric cues blocked, and was blocked by, learning about wall-colour information.

In stage 1 of Experiments 4, 5, and 6, participants were required to find a hidden goal within an arena that comprised 4 unique corners, each of which contained a distinctive landmark. Stage 2 of these experiments used entirely novel landmarks located in the corners of a differently-shaped arena, and participants again had to locate a hidden goal within the arena. Importantly, in both stages of the experiments, the landmarks did not maintain a fixed relationship with respect to the boundary walls of the environment. Consequently, either the shape of the arena, or the location of the landmarks, could be made relevant to navigating to the hidden goal. In each experiment, participants were faster to find the goal in stage 2 when the dimension relevant to finding the goal was the same as the relevant dimension in stage 1. These results were obtained when the landmarks were spatially integrated into the boundary of the arena (Experiment 4), or when they were spatially separated from the boundary as intra-maze cues (Experiments 5 and 6). Experiment 6 also revealed that participants' ability to recognise the shape of the arenas in which they had previously navigated was influenced by whether shape had been established as relevant to finding the goal, a result that will be discussed later on. The ID-ED effects noted in the experiments reported in Chapter 3 are inconsistent with the proposals of Miller and Shettleworth (2007, 2008, 2013), which assumes that the salience of a stimulus (α) is fixed. For an associative model to be capable of explaining ID-ED effects, changes in the attention paid to relevant and/or irrelevant dimensions must be permitted (Esber & Haselgrove, 2011; Le Pelley, 2004; Mackintosh, 1975).

In addition to providing an explanation for the ID-ED effects, attentional models, such as that proposed by Mackintosh (1975), also provide a potential reconciliation of the conflicting findings from spatial overshadowing experiments that were presented in the general introduction. According to Mackintosh's theory, cues with unconditionally high salience gain attention if they are learned about in compound with a cue that is of a lower unconditional salience, which itself will suffer a loss in attention. A cue that is more salient, therefore, will overshadow a less salient cue, but not vice versa. It is possible, then, that failures of a landmark to overshadow a boundary shape may be due to the landmark possessing low unconditional salience compared to the shape and, likewise, successes of landmarks overshadowing boundary shape may be due to the landmark possessing high unconditional salience compared to the shape. The learned predictiveness experiments reported in Chapter 4 were conducted to examine this argument.

In stage 1 of Experiment 7, participants were required to find a hidden goal located within an arena that comprised 4 unique corners, and that contained 4 distinctive landmarks. As with the ID-ED experiments, the landmarks did not maintain a fixed relationship with respect to the boundary walls of the environment. Consequently, either the shape of the arena, or the location of the landmarks, could be made relevant to navigating to the hidden goal. In stage 2 of Experiment 7, participants again had to locate a hidden goal within an arena that comprised 4 unique corners, and that contained 4 distinctive landmarks. Importantly, however, in stage 2 of Experiment 7 the location of the hidden goal was signalled with equal validity by both the unique geometry of a given corner and one of the distinctive landmarks. Conflict tests, which were used to avoid the confound of generalisation decrement that is present in overshadowing designs, demonstrated that the shape properties provided by the boundary walls of the stage 2 environment took control of behaviour if participants had received shape-relevance training in stage 1. In contrast, the landmark cues within the stage 2 arena took control of behaviour if participants had received landmark-relevance training in stage 1 of the experiment. The effect of relevance training appeared to be asymmetrical, however, with a greater bias in exploration in the landmark-relevant group. On the basis of this, it was proposed that the unconditional salience of the landmarks was greater than the shape properties provided by the stage 2 arena, and Experiment 8 confirmed this. When learning in stage 2 was preceded by no relevance training altogether, or training in which both shape and landmark cues were relevant, the landmark cues contained within the stage 2 arena took control of behaviour. The results of Experiment 7 demonstrate that it is possible to manipulate the cue dimension that takes control of navigational behaviour in stage 2 of the experiment, by preceding exploration of the stage 2 environment with relevance training in a different-shaped arena, which also contained different landmarks. These results provide a proof of concept to the idea that the differing results of spatial overshadowing experiments can be accounted for by the relative salience of landmark and boundary wall cues. The learned predictiveness effect, however, is again inconsistent with proposals of Miller and Shettleworth (2007, 2008, 2013) because of the assumption that the salience of a stimulus (α) is fixed. In order to account for these results, it would be necessary for the Miller-Shettleworth model to allow for changes in the attention paid to relevant and irrelevant stimuli, in a manner envisaged, for example, by Mackintosh (1975: see also Esber & Haselgrove, 2011; Le Pelley, 2004).

Returning now to the shape recognition task of Experiment 6, it was demonstrated that participants could recognise the global-shape of the environments in which they had navigated, a result that appears consistent with the notion that organisms encode a global representation of the shape and, thus, inconsistent with the idea that organisms learn about elements local to a rewarded corner (Miller & Shettleworth, 2007, 2008, 2013). The recognition task, although compelling, provided only a measure of global-shape knowledge, rather than a measure of the extent to which global-shape was used during navigation, or participants' knowledge of the goal location within the environment. Experiments 9 to 11 were, therefore, designed to assess the extent to which local- and global-shape representations are relied upon during navigation and, moreover, to assess whether a global representation that represents the Euclidean shape of an environment is encoded during navigation. In Experiments 9a and 9b, participants were trained to find a hidden goal in the right-angled corner of one side of an arena (e.g. an inside corner of a kite). At test, participants were placed on the alternate side of the same shape (e.g. the outside of the kite), and they spent more time exploring the right-angled corner that would have been closest to the goal signal during training. In Experiments 10a and 10b, participants were again trained to find a hidden goal on one side of an arena, before receiving a test on the alternate side of the arena. For Experiments 10a and 10b, however, the Euclidean shape of the training and test arenas was changed from a kite to a rectangle (or vice versa). Under these circumstances, participants displayed no preference for searching by either of the right-angled corners at test. Finally, Experiment 11 revealed that a change in only the shape of the arena between training and testing was not sufficient to disrupt transfer of navigation. Participants were trained to find a goal hidden by an exterior right-angled corner of one shape (e.g. a kite). At test, the global-shape of the arena was changed (e.g. to a rectangle) and, despite this change, participants preferentially searched by the right-angled corner that shared the same local-shape cues on the outside of a rectangle (See also Experiment 1).

As noted previously, it is difficult to explain the results of Experiments 9 to 11 by assuming that organisms encode only one representation of the space they navigate in, as the results of at least one of the experiments are inconsistent with theories of navigation based on local-shape information, Euclidian shape information, or the principal axis of an environment. It was, therefore, necessary to invoke multiple representations of environmental geometry in order to successfully explain the data reported in Experiments 9 to 11. Importantly, in order to account for these data, it appeared necessary to assume that organisms encode a Euclidean representation of the shape of the environment in which they navigate, in a manner envisaged by proponents of the geometric module. Encoding of such a representation is consistent with the finding that participants recognised the shape of the environments that they have previously navigated within. Again, however, this is not consistent with the Miller-Shettleworth model of spatial navigation, a theory which rules out learning about a global representation of the shape of an environment.

In summary, in order to account for the results presented in this thesis, models of spatial navigation must permit humans to encode multiple representations of the shape of the environments in which they navigate. At the very least, that data reported in this thesis demonstrates that humans navigate on the basis of both local geometric cues (Experiment 1) and a global representation of the Euclidean shape of the environment (Experiment 9). Data reviewed in the introduction to this thesis also suggests that humans are able to navigate on the basis of the principal axis of an environment (Bodily et al., 2011). Importantly, a converging conclusion from the experiments in Chapters 2-4, is that models of spatial navigation must permit multiple representations of the shape of the environment to be susceptible to changes in the attention paid to them. As discussed earlier, the ID-ED and learned predictiveness effects that were observed can only be explained by models of associative learning that permit changes in the attention paid to cues (e.g. Esber &

Haselgrove, 2010; Le Pelley, 2004; Mackintosh, 1975). In suggesting that the attention paid to local geometric cues is susceptible to changes in attention, it is then possible to account for the blocking results observed in Experiments 2 and 3 by assuming that the attention paid to the blocking cue was greater than the attention paid to the to-be-blocked cue in stage 2 of those experiments. As noted above, the data from the shape recognition test of Experiment 6 suggests that global representations of the shape of an environment are also susceptible to variations in attention.

Taken together, the data in this thesis are not consistent with (a) theories of navigation that afford the boundary shape of an environment a special status during learning, such that organisms are predicted to always learn about the boundaries of their environment (Doeller & Burgess, 2008; Cheng, 1986; Gallistel, 1990; Wang & Spelke 2002, 2003), (b) cognitive mapping theories that suggest learning about navigational cues should occur without interference (e.g. O'Keefe & Nadel, 1978), (c) theories which do not permit changes in the attention paid to cues (e.g. Miller & Shettleworth, 2007, 2008, 2013), or (d) suggestions that animals navigate only on the basis of local-shape information (e.g. Pearce et al., 2004). The challenge for future work will be to determine the manner in which multiple representations of the shape of an environment are used to support navigational behaviour, and how these representations interact with other navigational cues such as landmarks. Some suggestions for experiments that will aid understanding this issue are described in the following section.

6.1 Future work

6.1.1 Multiple representations of shape.

The geometric module hypothesis suggests that 1) organisms encode a global representation of the shape of the environment in which they navigate, and 2) that this representation is immune to interference from other cues, such as landmarks. As noted throughout this thesis, a number of experiments have found that landmarks can overshadow, and block, learning about the shape of an environment. As explained in Chapter 2, however, the training and testing phases of these experiments have been conducted in the same-shaped environments; thus, it is not possible to determine whether these experiments have demonstrated cue competition effects between local- or global-shape representations, and landmarks. The inside-outside paradigm presented in Chapter 5 provides a method to dissociate navigation based on global-shape parameters from that based on local-shape parameters and, taken together, the data from Experiments 9 to 11 provide evidence that humans encode a global Euclidean representation of the shape of the environments in which they navigate. In Experiment 9a, participants were trained to find a hidden goal on the inside of an arena, before receiving a test trial on the outside of the same-shaped arena. During this test trial, participants spent more time searching at the exterior corner of the shape that was consistent with navigating on the basis of a Euclidean representation of the shape of the environment, compared to the time they spent searching at the corner that was consistent with navigating on the basis of local-shape information. Given that the test behaviour of participants was driven by Euclidean representation of the shape of the environment, it would be possible to adapt this design to determine whether this global-shape representation could be overshadowed, or blocked, by landmark cues.

To assess overshadowing of Euclidean shape representations, it would be necessary to introduce landmark cues that signal the goal location during the training stage of this experiment, before testing search behaviour on the outside of the arena in the absence of these landmarks. During acquisition, participants could learn the location of the hidden goal based on information provided by the shape of the environment, as well as by information provided by the landmarks. A control group would receive training where only the shape of the environment predicted the goal location. In order to protect against the confounding effect of generalisation decrement (Pearce, 1987), it would be necessary to present landmarks to control participants also. In order to ensure that the landmarks do not signal the goal location for the control group, it would be necessary to either (a) place identical landmarks at both goal and non-goal locations (e.g. Haywood et al., 2004; McGregor et al., 2009; Redhead & Hamilton, 2009), or (b) move the landmarks on every trial (e.g. Horne et al., 2011; Horne & Pearce, 2011: see also group shape-shape of Experiments 4, 5, and 6). Following this training, both groups would receive a test trial on the outside of the same-shaped environment. Participants in the control group would be expected to demonstrate a preference for searching at the corner consistent with navigating on the basis of a Euclidean representation of the shape of the environment, over the corner consistent with navigating on the basis of local-shape information, as was reported in Experiment 9a. If participants in the overshadowing group displayed a significantly attenuated preference for this corner, relative to the control group, then the presence of the predictive landmarks during training must have interfered with the encoding of a global Euclidean representation of the shape of the environment. At the time at which this thesis was submitted, data collection for an experiment assessing whether the acquisition of a global representation of the shape of an environment was prone to overshadowing had already begun (see Figure 6.1).

To assess whether landmarks can block learning about the global-shape of the environment, participants in a blocking and a control group could first be trained to navigate to a hidden goal located near one of four landmarks. These landmarks could be presented in an open grassy plain, such that no other cues were present. In stage 2 of the experiment, the same landmarks would be presented inside the corners of, say, a kite-shaped arena. For participants in the blocking group, the hidden goal would remain next to the landmark that previously signalled the goal location. Consequently, these participants would not be expected to learn about the corner of the kite-shaped arena that also signalled the goal location. For control participants, however, the goal would be located near a landmark that previously did not signal the goal location and, thus, these participants may be expected to learn about the corner of the kite-shaped arena that now signals the goal location. Alternatively, it would be possible to conduct this experiment with a control group that is trained in the same manner as the overshadowing group in Figure 6.1. Again, test trials would be conducted on the outside of the same-shaped arena in the absence of any landmarks. During this test, control participants would be expected to search at the corner of the environment consistent with navigating on the basis of a Euclidean representation of the shape over the corner of the environment consistent with navigating on the basis of local-shape cues. Any attenuation of this preference in the blocking group, relative to the control group, would indicate that the landmarks had interfered with the encoding of a global Euclidean representation of the shape of the environment.

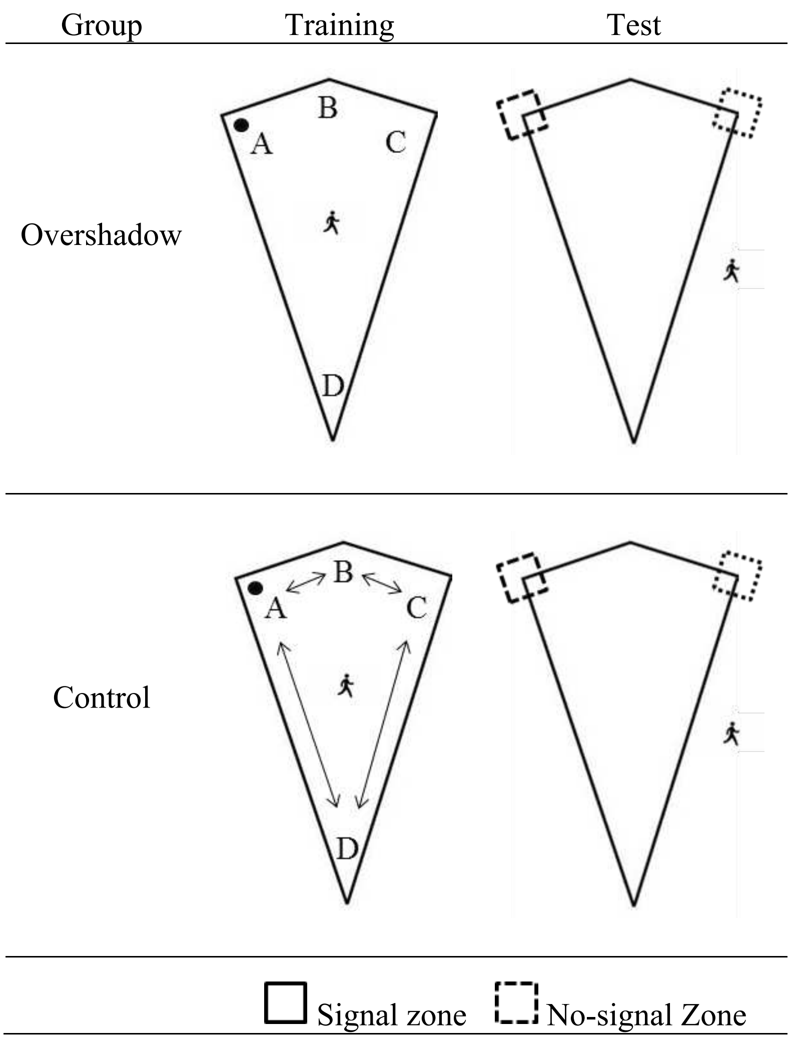


Figure 6.1. Schematic views of the arenas used to assess if a global-shape representation can be overshadowed by landmarks. Black circles represent the hidden goal, and square search zones are superimposed on the diagram of the test environment. The location of the person indicates whether participants were navigating on the inside, or the outside, of the arena. Letters A, B, C, and D represent different landmarks. The arrows between the landmarks for the control condition represent the fact that they change position on every trial.

In Experiments 9 and 10, the training environments were different from the testing environments. For example, in Experiment 9a, participants were trained to navigate to a concave corner on the inside of a shape that had wooden floor and cream walls. Following this, participants received a test trial on the outside of the shape, a context that had convex corners, a brick texture applied to the walls, and a grass floor. During this test trial, participants searched in the corner of the environment consistent with navigating on the basis of the global-shape of the environment, over the corner consistent with navigating on the basis of local-shape cues. It is, however, possible that local-shape representations are sensitive to substantial changes in the elements that construct them, or encoded in an egocentric manner. If this is so, then it is of little surprise that they did not control behaviour during the test trial. In order to test these possibilities, and to assess if local-shape representations can be transferred from the inside to the outside of an environment, it would be necessary to reduce the difference between training and the test environments on the inside-outside paradigm reported in Chapter 5. To achieve this, participants could be trained to find a Wi-Fi signal inside of a cross-shaped environment, before being tested on the outside of the same shape. Importantly, both the training and test environments would contain concave and convex corners, and it would be possible to ensure that both environments had, say, cream coloured walls and a grass texture applied to the floor. As shown in Figure 6.2, the test trial of this experiment would contain corners that share the exact same local representation that was rewarded during training. It might, then, be expected participants spend an equal amount of time searching at the corners consistent with navigating on the basis of local-shape cues compared to the time spent searching at the corners consistent with navigating on the basis of the global-shape of the environment. At the very least, reducing the difference between the training and test environments could lead to an attenuation of the effect observed in Experiment 9a. At the time this thesis was submitted, data collection for this experiment had begun.

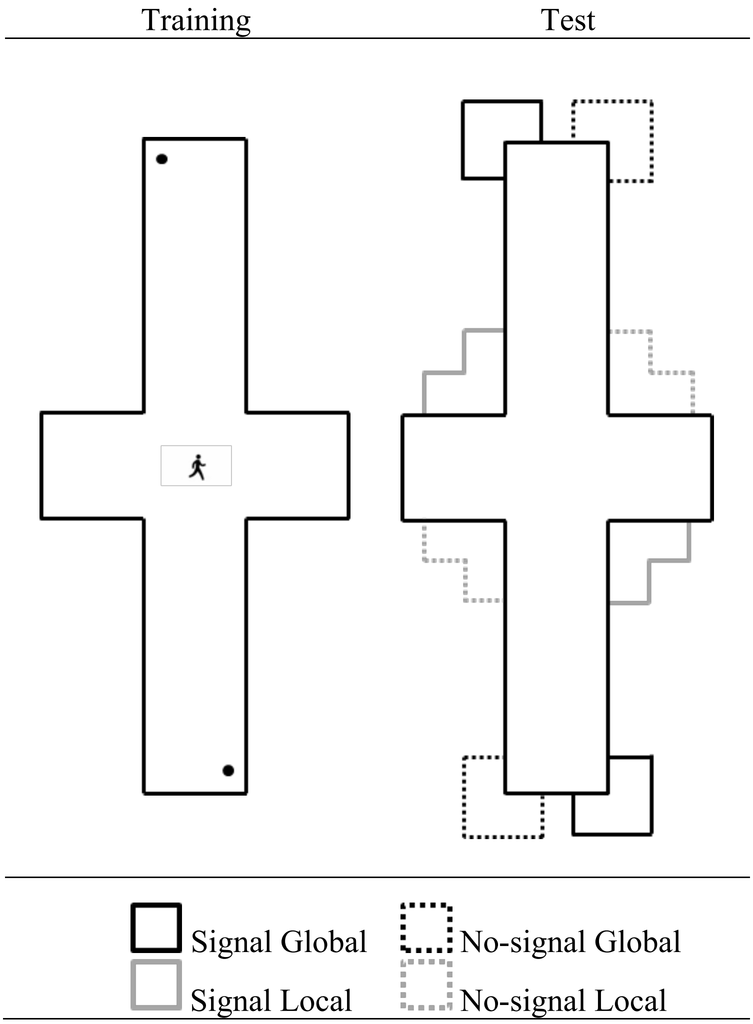


Figure 6.2. Schematic views of arenas used to assess if local geometric cues are sensitive to generalization decrement. Black circles represent the location of a hidden goal, and search zones are superimposed on the diagram of the test environment. The location of the person indicates whether participants were navigating on the inside, or the outside, of the arena.

6.1.2 The role of language in human navigation.

Throughout this thesis, the discussion of results has been largely focussed on theories of navigation that are assumed to be species-universal (e.g. Cheng, 1986; Gallistel, 1990; Miller & Shettleworth 2007, 2008, 2013). It is, however, appropriate to also consider the role of more explicit, verbally mediated, processing mechanisms that may guide navigation in adult humans. More specifically, in the experiments reported in this thesis, it is conceivable that participants may have acquired declarative statements that they used to guide navigation. Take, for instance, Experiments 4-7, in which it is possible that participants in groups that received training in stage 1 in which the shape of the arena was relevant to finding the goal (groups shape-shape and shape-landmark in Experiments 4-6, and group shape-relevant in Experiment 7) may have acquired a declarative statement in the first stage of the experiment that "the goal is located in the corner of the arena where the long wall is to the left of the short wall, irrespective of the colour of the landmark that is there – so ignore that". Acquisition of such a statement could be expected to facilitate subsequent learning that is based upon the shape of a new environment and, in contrast, impede subsequent learning that is based upon landmarks (Experiments 4-6). Such a statement might also be expected to promote learning about the shape information of a novel environment, at the expense of learning about the landmarks within the novel environment (group shape-relevant of Experiment 7). Finally, a verbal statement that makes direct reference to shape features of the environment might also be expected to facilitate performance on the shape recognition task in Experiment 6; however, a verbal statement that "the goal is located by the darkest blue landmark, irrespective of what corner it is in" would be expected to attenuate performance on the same task.

It is also possible that navigation in the experiments reported in Chapter 2 may have been verbally mediated. For instance, participants in Experiment 1 may have verbally encoded a rule that "the goal is located in the corner of the arena where the long wall is to the left of the short wall". Acquisition of such a statement could then explain the transfer of navigational behaviour between environments that share the same local geometric cues. Encoding such a rule might also be expected to increase the attention paid to shape cues in a novel environment, similar to Experiment 7. Initial training in which participants encode a verbal rule based on local geometric cues might, therefore, be expected to attenuate subsequent learning about wall colour information (Experiment 3) and, likewise, encoding a rule based on wall colour information might be expected to attenuate learning of geometric information (Experiment 2)

An experiment conducted by Hermer-Vazquez, Spelke & Katsnelson (1999) provides support for the role of explicit linguistic mechanisms in spatial navigation. They required adult participants to locate a hidden goal in a rectangle-shaped room that had a blue panel attached to one of the shorter walls. Performance on this task was significantly attenuated when it was performed along with a verbal shadowing task, but not a nonverbal rhythm-clapping task. It should be noted, however, that an attempt to replicate this effect by Hupbach, Hardt, Nadel and Bohot (2007) was not successful. Similarly, Ratliff & Newcombe (2008b) were unable to replicate the results reported by Hermer-Vazquez et al. when the experiment was appropriately counterbalanced, and preceded by clear instructions and a practice trial. Perhaps most problematic for advocates of the role of verbal mechanisms in spatial navigation is the observation that performance on the task described by Hermer-Vazquez et al. is comparable in participants with and without aphasia, even under conditions of verbal load where, presumably, any residual verbal competency in participants with aphasia is blocked (Bek, Blades, Siegal & Varley, 2010).

As well as acquisition of declarative statements during navigation, there is also evidence to suggest that the language used to instruct participants may influence their spatial navigational behaviour. Hardt, Hupback, and Nadel (2009) conducted a series of blocking experiments in which participants were required to navigate within a circular environment to find a hidden goal, the location of which was signalled by extra-maze landmarks. In stage 1, participants in a blocking group only received training in which they had to locate a hidden goal with respect to one set of distal landmarks (set A). In stage 2, a novel set of distal landmarks (set B) were added to the environment, and participants in both the blocking and control groups received compound training in which both sets of landmarks signalled the goal location. Finally, participants in both groups received test trials, in which the hidden goal was removed, conducted only with the landmark cues that had been added to the environment in stage 2 (set B). In one experiment, participants received the instructions presented in the top panel of Table 6.1. Here, participants in the blocking group spent significantly less time searching in the quadrant of the arena that had previously contained the hidden goal, relative to the control group. In a second experiment, participants received the instructions presented in the bottom panel of Table 6.1. With these instructions, participants in the blocking and control groups spent an equivalent amount of time searching in the quadrant of the arena that had previously contained the goal; thus, a blocking effect was not observed.

Based on the results noted above, Hardt et al. (2009) suggested that the instructions used to describe a task will influence the navigation strategy of participants. In order to form a cognitive map, it is necessary to provide statements that encourage exploratory behaviour in participants and, moreover, to also inform them that the goal will remain in the same location on every trial (see top panel of Table 6.1). In the absence of these statements, participants will only learn to approach the distal cues that are closest to the goal location. Task instructions, therefore, appear to determine whether the locale or taxon navigational system (O'Keefe & Nadel, 1978) will control behaviour. The instructions used in all the experiments conducted in this thesis, crucially, contain the necessary statements that, according to Hardt et al. (2009), should elicit the formation of a cognitive map. As noted in the general discussions of Chapters 2-4, however, the results of experiments 1-8 are not consistent with the notion that organisms encode a global allocentric map of the shape of the environment in which they navigate. Consequently, including the key statements identified by Hardt et al. (2009) in the instructions used in the experiments reported in this thesis was not sufficient to generate navigational behaviour consistent with cognitive mapping theories.

Table 6.1. Instructions that do (top), and do not (bottom), promote the formation of a cognitive map during human navigation experiments conducted in a virtual environment. The italic lettering in the top panel highlights the crucial information that, according to Hardt et al. (2009), determines whether or not participants form a cognitive map of their environment.

Instructions that favour the formation of a cognitive map
Your task is to find a large pink square, the "target". The target will be invisible until you step on it – then the target will become visible. You will know that you stepped on the target when you hear a clicking sound and you will also see the target appear on the floor – it is a pink square. You will also be trapped, so that you cannot move off the target once you are on it. *The target will always be in the same location. The pictures on the wall of the room will help you to find the target. So have a good look around you each time you find the target – that will help you to quickly find the target again in the next trial.*
Instructions that do not favour the formation of a cognitive map
Your task is to find a large pink square, the "target". The target will be invisible until you step on it – then the target will become visible. You will know that you stepped on the target when you hear a clicking sound and you will also see the target appear on the floor – it is a pink square. You will also be trapped, so that you cannot move off the target once you are on it.

On the basis of the data reviewed above, there is not compelling evidence that language influences performance on the tasks reported in this thesis, either through explicit verbal encoding during navigation or the phrasing of task instructions. Nevertheless, in order to assess whether performance on the experiments contained within this thesis was mediated by verbal encoding, it would be necessary to conduct further research. To determine the extent to which performance in the experiments reported in this thesis was mediated by verbal processes, it would be necessary to repeat the navigational tests, and combine them with a concurrent verbal shadowing task. In order to control for working memory load, navigational performance under verbal load would then be compared to an appropriately matched non-verbal control task, such as concurrent tapping of a rhythm (e.g. Hermer-Vasquez et al., 1999). A significant deficit in the verbal shadowing group, relative to the non-verbal shadowing group, would suggest verbal processes were influencing performance on the tasks reported in this thesis.

6.1.3 Real- versus virtual-world navigation.

The experiments reported in this thesis were all conducted in a virtual-environment, and there were two reasons for this. First, the cost of building the real-world equivalents of the experiments reported here would be prohibitive. Second, conducting experiments in a virtual-world offers a level of control over the environment that is simply not possible to obtain in real-world experiments (e.g. extraneous noise, light, and smells might confound experiments conducted in the real-world). It might, nevertheless, be reasonable to question whether the effects observed in the experiments reported here are relevant to organisms navigating in the real-world. It should, however, be reassuring that effects observed in humans navigating in a virtual-world have also been reported in real-world experiments that have been conducted with animal subjects. For instance, in Experiment 1 it was demonstrated that humans navigating in a virtual kite-shaped arena transferred local-shape information to a virtual rectangle-shaped arena (see also Lew et al., 2014), an effect that was first observed in rats navigating in a water-maze (Pearce et al., 2004). In Experiment 2, it was observed that learning about landmark information blocked subsequent learning about shape information in humans navigating in a virtual-world (see also Wilson & Alexander, 2008), and similar effects have been reported in studies conducted with rats (e.g. Pearce et al., 2006). Finally, the ID-ED effects reported in Experiments 4-6 have also been obtained with rats (Cuell et al., 2012).

Beyond the results reported in this thesis, it is also worthwhile to note that the same brain structures that are known to be involved during navigation based on the boundary shape of an environment in rats, namely, the hippocampus (e.g. Horne et al., 2010), have been shown to be active in human participants navigating on the basis of the boundaries of a virtual environment (e.g. Doeller et al., 2008). Similarly, para-hippocampal regions have been shown to be implicated in learning about landmarks in rats (e.g. Kosaki, Poulter, Austen, & McGregor, 2015; Save & Poucet, 2000) and also in humans learning about landmarks in a virtual environment (e.g. Doeller & Burgess, 2008; Sutton, Joanisse, & Newcombe, 2010). It appears then, at least at face value, that humans navigating through a virtual environment recruit the same neural structures, and presumably, therefore, similar processes, as rats recruit when navigating in a water-maze.

It must be noted that there are clear differences between navigating in a computer environment and navigating in real life. The sensory input entering the navigational system differs in virtual-world experiments compared with real-world experiments. For instance, organisms receive vestibular, proprioceptive, and somesthetic inputs during real-world experiments, but not in virtual reality experiments (Lavenex & Lavenex, 2010). The experiments contained within this thesis, though, were not designed to test if the additional navigational input that is received when navigating in a real-world environment would result in different spatial behaviour, compared to navigation in a virtual-world. Consequently, additional research will be required to address this issue. A simple, but costly, manner in which to test for differences in real- and virtual-world navigation would be to replicate the design of the experiments presented in this thesis in a controlled real-world environment. An additional avenue of research would be to conduct experiments using virtual-reality technology such as Oculus rift. Using such a head-mounted display, participants can physically walk around a large empty room in order to navigate through a computer generated environment. Experimenters would, therefore, maintain the strict level of control over variables that is offered by computer generated environments. In addition, using this technology also makes it possible for participants to receive vestibular, proprioceptive, and somesthetic input to navigational system.

6.2 Conclusion

The aim of this thesis was to test three key predictions derived from the model proposed by Miller and Shettleworth (2007, 2008, 2013): First, that learning about local geometric information competes with non-geometric information for associative strength; Second, that the salience of cues within the environment is not modifiable; Third, that animals do not learn about a global representation of the shape of an environment. Taken together, the data reported in this thesis suggest that, at best, the model of spatial navigation proposed by Miller and Shettleworth (2007, 2008, 2013) provides an incomplete explanation of spatial learning phenomena. The results of the blocking experiments presented in Chapter 2 are consistent with the first prediction outlined above. However, the ID-ED and learned predictiveness effects observed in Chapter 3 and 4, respectively, suggest that it is necessary for the Miller-Shettleworth model to permit changes in the attention paid to stimuli in the manner envisaged by Mackintosh (1975: see also Esber & Haselgrove, 2010; Le Pelley, 2004). By allowing the attention paid to a stimulus to be modified by the unconditional salience of its elements, as well as learning with respect to those elements, it is likely that the Miller-Shettleworth model could account for the results reported in Chapter 3 and 4. The results reported in Chapter 5, however, are particularly problematic for theories that assume that organisms learn about elements local to a rewarded corner, such as the model proposed by Miller and Shettleworth (2007, 2008, 2013), as it appears necessary to assume that organisms learn about a global Euclidean representation of the shape of the environments in, or around, which they navigate. The challenge for future work, therefore, will be to determine the precise manner in which multiple representations of environmental geometry support effective navigation, and how these representations interact with non-geometric information, such as landmarks.

References

Austen, J. M., Kosaki, Y., & McGregor, A. (2013). Within-compound associations explain potentiation and failure to overshadow learning based on geometry by discrete landmarks. *Journal of Experimental Psychology: Animal Behavior Processes, 39*(3), 259-272.

Ayaz, H., Allen, S. L., Platek, S. M., & Onaral, B. (2008). Maze Suite 1.0: A complete set of tools to prepare, present, and analyze navigational and spatial cognitive neuroscience experiments. *Behavior Research Methods, 40*(1), 353-359.

Bek, J., Blades, M., Siegal, M., & Varley, R. (2010). Language and Spatial Reorientation: Evidence From Severe Aphasia. *Journal of Experimental Psychology: Learning Memory and Cognition, 36*(3), 646-658.

Biederman, I. (1987). Recognition by components: a theory of human image understanding. *Psychological Review, 94*(2), 115-147.

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*(3), 334-351.

Bitterman, M. E. (2000). Cognitive evolution: A psychological perspective. In C. M. Heyes & L. Huber (Eds.), *The evolution of cognition*. Cambridge, MA: MIT Press.

Blough, D. S. (1975). Steady state data and a quantitative model of operant generalization and discrimination. *Journal of Experimental Psychology: Animal Behavior Processes*, *1*(1), 3-21.

Bodily, K. D., Eastman, C. K., & Sturz, B. R. (2011). Neither by global nor local cues alone: evidence for a unified orientation process. *Animal Cognition, 14*(5), 665-674.

Bouton, M. E. (2007). *Learning and behavior: A contemporary synthesis*. Sunderland, MA, US: Sinauer Associates.

Bullens, J., Nardini, M., Doeller, C. F., Braddick, O., Postma, A., & Burgess, N. (2010). The role of landmarks and boundaries in the development of spatial memory. *Developmental Science, 13*(1), 170-180.

Burgess, N. (2006). Spatial memory: how egocentric and allocentric combine. *Trends in Cognitive Sciences, 10*(12), 551-557.

Burgess, N. (2008). Spatial Cognition and the Brain. *Annals of the New York Academy of Sciences, 1124*(1), 77-97.

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*(3), 262-281.

Chamizo, V. D., Manteiga, R. D., Rodrigo, T., & Mackintosh, N. J. (2006). Competition between landmarks in spatial learning: The role of proximity to the goal. *Behavioural Processes, 71*(1), 59-65.

Cheng, K. (1986). A purely geometric module in the rats spatial representation. *Cognition, 23*(2), 149-178.

Cheng, K. (2005). Reflections on geometry and navigation. *Connection Science, 17*(1-2), 5-21.

Cheng, K. (2008). Whither geometry? Troubles of the geometric module. *Trends in Cognitive Sciences, 12*(9), 355-361.

Cheng, K., & Gallistel, C. R. (2005). Shape parameters explain data from spatial transformations: Comment on Pearce et al. (2004) and Tommasi & Polli (2004). *Journal of Experimental Psychology: Animal Behavior Processes, 31*(2), 254-259.

Cheng, K., Huttenlocher, J., & Newcombe, N. S. (2013). 25 years of research on the use of geometry in spatial reorientation: A current theoretical perspective. *Psychonomic Bulletin and Review, 20*, 1033-1054.

Cheng, K., & Newcombe, N. S. (2005). Is there a geometric module for spatial orientation? Squaring theory and evidence. *Psychonomic Bulletin and Review, 12*(1), 1-23.

Cheng, K., Shettleworth, S. J., Huttenlocher, J., & Rieser, J. J. (2007). Bayesian integration of spatial information. *Psychological Bulletin, 133*(4), 625.

Cheng, K., & Spetch, M. (2001). Blocking in landmark-based search in honeybees. *Animal Learning and Behavior, 29*(1), 1-9.

Cheng, K., & Spetch, M. L. (1998). Mechanisms of landmark use in mammals and birds *Spatial representation in animals* (pp. 1-17). New York, NY, US: Oxford University Press.

Cheung, A., Stuerzl, W., Zeil, J., & Cheng, K. (2008). The information content of panoramic images II: View-based navigation in nonrectangular experimental arenas. *Journal of Experimental Psychology: Animal Behavior Processes, 34*(1), 15-30.

Christou, C. G., & Bulthoff, H. H. (1999). View dependence in scene recognition after active learning. *Memory and Cognition, 27*(6), 996-1007.

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*(2), 99-112.

Couvillon, P. A., Campos, A. C., Bass, T. D., & Bitterman, M. E. (2001). Intermodal blocking in honeybees. *Quarterly Journal of Experimental Psychology Section B: Comparative and Physiological Psychology, 54*(4), 369-381.

Cuell, S. F., Good, M. A., Dopson, J. C., Pearce, J. M., & Horne, M. R. (2012). Changes in attention to relevant and irrelevant stimuli during spatial learning. *Journal of Experimental Psychology: Animal Behavior Processes, 38*(3), 244-254.

Denton, S. E., & Kruschke, J. K. (2006). Attention and salience in associative blocking. *Learning and Behavior, 34*(3), 285-304.

Dickinson, A., Hall, G., & Mackintosh, N. J. (1976). Surprise and the attenuation of blocking. *Journal of Experimental Psychology: Animal Behavior Processes, 2*(4), 313–322.

Dienes, Z. (2008). *Understanding psychology as a science: An introduction to scientific and statistical inference*. Basingstoke: Palgrave Macmillan.

Dienes, Z. (2011). Bayesian versus orthodox statistics: Which side are you on? *Perspectives on Psychological Science, 6*(3), 274-290.

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 of the United States of America, 105*(15), 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 of the United States of America, 105*(15), 5915-5920.

Duffaud, A. M., Killcross, S., & George, D. N. (2007). Optional-shift behaviour in rats: A novel procedure for assessing attentional processes in discrimination learning. *The Quarterly Journal of Experimental Psychology*, *60*(4), 534-542.

Esber, G. R., & Haselgrove, M. (2011). Reconciling the influence of predictiveness and uncertainty on stimulus salience: a model of attention in associative learning. *Proceedings of the Royal Society B: Biological Sciences, 278*(1718), 2553-2561.

Esber, G. R., McGregor, A., Good, M. A., Hayward, A., & Pearce, J. M. (2005). Transfer of spatial behaviour controlled by a landmark array with a distinctive shape. *Quarterly Journal of Experimental Psychology Section B: Comparative and Physiological Psychology, 58*(1), 69-91.

Farah, M. J., Rochlin, R., & Klein, K. L. (1994). Orientation invariance and geometric primitives in shape-recognition. *Cognitive Science, 18*(2), 325-344.

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.

Fodor, J. A. (1983). *The modularity of mind: An essay on faculty psychology*. Cambridge, Mass.: MIT Press.

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

Gallistel, C. R., & Matzel, L. D. (2013). The Neuroscience of Learning: Beyond the Hebbian Synapse. *Annual Review of Psychology, 64*, 169 - 200.

George, D. N., & Pearce, J. M. (1999). Acquired distinctiveness is controlled by stimulus relevance not correlation with reward. *Journal of Experimental Psychology: Animal Behavior Processes, 25*(3), 363-373.

George, D. N., Ward-Robinson, J., & Pearce, J. M. (2001). Discrimination of structure: I. Implications for connectionist theories of discrimination learning. *Journal of Experimental Psychology: Animal Behavior Processes, 27*(3), 206-218.

Gould-Beierle, K. L., & Kamil, A. C. (1999). The effect of proximity on landmark use in Clark's nutcrackers. *Animal Behaviour, 58*, 477-488.

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 the environment is influenced by properties of the objects forming the shape. *Journal of Experimental Psychology: Animal Behavior Processes, 32*(1), 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*(3), 314-317.

Hall, G., Mackintosh, N. J., Goodall, G., & Dalmartello, M. (1977). Loss of control by a less valid or by a less salient stimulus compounded with a better predictor of reinforcement. *Learning and Motivation, 8*(2), 145-158.

Hamilton, D. A., Johnson, T. E., Redhead, E. S., & Verney, S. R. (2009). Control of rodent and human spatial navigation by room and apparatus cues. *Behavioural Processes, 81*(2), 154-169.

Hardt, O., Hupback, A., & Nadel, L. (2009). Factors moderating blocking in human place learning: The role of task instructions. *Learning and Behavior, 37*(1), 42-59.

Haselgrove, M., George, D. N., & Pearce, J. M. (2005). The discrimination of structure: III. Representation of spatial relationships. *Journal of Experimental Psychology: Animal Behavior Processes, 31*(4), 433-448.

Haselgrove, M., Tam, S. K. E., & Jones, P. M. (2013). Enhanced unblocking from sustained post-trial surprise. *Journal of Experimental Psychology: Animal Behavior Processes*, *39*(4), 311-322.

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 Section B: Comparative and Physiological Psychology, 57*(4), 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 Section B: Comparative and Physiological Psychology, 56*(1), 114-126.

Hermer-Vazquez, L., Moffet, A., & Munkholm, P. (2001). Language, space, and the development of cognitive flexibility in humans: the case of two spatial memory tasks. *Cognition, 79*(3), 263-299.

Hermer-Vazquez, L., Spelke, E. S., & Katsnelson, A. S. (1999). Sources of flexibility in human cognition: Dual-task studies of space and language. *Cognitive Psychology, 39*(1), 3-36.

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

Hermer, L., & Spelke, E. S. (1994). A geometric process for spatial reorientation in young-children. *Nature, 370*(6484), 57-59.

Hock, H. S., & Schmelzkopf, K. F. (1980). The abstraction of schematic representations from photographs of real-world scenes. *Memory and Cognition, 8*(6), 543-554.

Holland, P. C. (1984). Unblocking in Pavlovian appetitive conditioning. *Journal of Experimental Psychology: Animal Behavior Processes*, *10*(4), 476-497.

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*(5), 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*(2), 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*(1), 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*(3), 381-394.

Horne, M. R., & Pearce, J. M. (2011). Potentiation and overshadowing between landmarks and environmental geometric cues. *Learning and Behavior, 39*(4), 371-382.

Hupbach, A., Hardt, O., Nadel, L., & Bohbot, V. D. (2007). Spatial reorientation: Effects of verbal and spatial shadowing. *Spatial Cognition and Computation, 7*(2), 213-226.

Hupbach, A., & Nadel, L. (2005). Reorientation in a rhombic environment: No evidence for an encapsulated geometric module. *Cognitive Development, 20*(2), 279-302.

Jeffery, K. J. (2010). Theoretical accounts of spatial learning: A neurobiological view (commentary on Pearce, 2009). *Quarterly Journal of Experimental Psychology, 63*(9), 1683-1699.

Jeffreys, H. (1961). Theory of probability: Oxford University Press, Oxford UK.

Kamin, L. J. (1969). Selective association and conditioning. In N. J. Mackintosh & W. K. Honig (Eds.), *Fundamental issues in associative learning* (pp. 42 - 64). Halifax, Nova Scotia, Canada: Dalhousie University Press.

Kelly, D. M., Chiandetti, C., & Vallortigara, G. (2010). Re-orienting in space: do animals use global or local geometry strategies? *Biology Letters, 7*(3), 372-375.

Kelly, D. M., Spetch, M. L., & Heth, C. D. (1998). Pigeons' (Columba livia) encoding of geometric and featural properties of a spatial environment. *Journal of Comparative Psychology, 112*(3), 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.

Kosaki, Y., Poulter, S. L., Austen, J. M., & McGregor, A. (2015). Dorsolateral striatal lesions impair navigation based on landmark-goal vectors but facilitate spatial learning based on a “cognitive map”. *Learning and Memory, 22*(3), 179-191.

Lavenex, P. B., & Lavenex, P. (2010). Spatial relational learning and memory abilities do not differ between men and women in a real-world, open-field environment. *Behavioural Brain Research, 207*(1), 125-137.

Le Pelley, M. E. (2004). The role of associative history in models of associative learning: A selective review and a hybrid model. *Quarterly Journal of Experimental Psychology Section B: Comparative and Physiological Psychology, 57*(3), 193-243.

Le Pelley, M. E. (2010). Attention and human associative learning. In C. J. Mitchell & M. E. Le Pelley (Eds.), *Attention and Associative Learning: From Brain to Behaviour* (pp. 131 - 158). Oxford, UK: Oxford University Press.

Le Pelley, M. E., Beesley, T., & Griffiths, O. (2011). Overt Attention and Predictiveness in Human Contingency Learning. *Journal of Experimental Psychology: Animal Behavior Processes, 37*(2), 220-229.

Le Pelley, M. E., & McLaren, I. P. L. (2003). Learned associability and associative change in human causal learning. *Quarterly Journal of Experimental Psychology Section B: Comparative and Physiological Psychology, 56*(1), 68-79.

Le Pelley, M. E., Vadillo, M., & Luque, D. (2013). Learned predictiveness influences rapid attentional capture: Evidence from the dot probe task. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *39*(6), 1888-1900.

Learmonth, A. E., Nadel, L., & Newcombe, N. S. (2002). Children's use of landmarks: Implications for modularity theory. *Psychological Science, 13*(4), 337-341.

Learmonth, A. E., Newcombe, N. S., & Huttenlocher, J. (2001). Toddlers' use of metric information and landmarks to reorient. *Journal of Experimental Child Psychology, 80*(3), 225-244.

Learmonth, A. E., Newcombe, N. S., Sheridan, N., & Jones, M. (2008). Why size counts: children's spatial reorientation in large and small enclosures. *Developmental Science, 11*(3), 414-426.

Lee, S. A., Sovrano, V. A., & Spelke, E. S. (2012). Navigation as a source of geometric knowledge: Young children's use of length, angle, distance, and direction in a reorientation task. *Cognition, 123*(1), 144-161.

Leising, K., Wong, J., Ruprecht, C., & Blaisdell, A. (2014). Blocking between landmarks during 2-D (touchscreen) and 3-D (ARENA) search tasks with pigeons. *Learning and Behavior, 42*(4), 357-364.

Leising, K. J., Garlick, D., & Blaisdell, A. P. (2011). Overshadowing Between Landmarks on the Touchscreen and in ARENA With Pigeons. *Journal of Experimental Psychology: Animal Behavior Processes, 37*(4), 488-494.

Lew, A. R. (2011). Looking Beyond the Boundaries: Time to Put Landmarks Back on the Cognitive Map? *Psychological Bulletin, 137*(3), 484-507.

Lew, A. R., Usherwood, B., Fragkioudaki, F., Koukoumi, V., Smith, S. P., Austen, J. M., & McGregor, A. (2014). Transfer of spatial search between environments in human adults and young children (Homo sapiens): Implications for representation of local geometry by spatial systems. *Developmental Psychobiology, 56*(3), 421-434.

Livesey, E. J., Harris, I. M., & Harris, J. A. (2009). Attentional Changes During Implicit Learning: Signal Validity Protects a Target Stimulus

From the Attentional Blink. *Journal of Experimental Psychology: Learning Memory and Cognition, 35*(2), 408-422.

Loomis, J. M., Klatzky, R. L., Golledge, R. G., Cicinelli, J. G., Pellegrino, J. W., & Fry, P. A. (1993). Nonvisual navigation by blind and sighted: assessment of path integration ability. *Journal of Experimental Psychology: General, 122*(1), 73-91.

Lourenco, S. F., & Huttenlocher, J. (2007). Using geometry to specify location: Implications for spatial coding in children and nonhuman animals. *Psychological Research*, *71*(3), 252-264.

Lourenco, S. F., Huttenlocher, J., & Vasilyeva, M. (2005). Toddlers' Representations of Space: The Role of Viewer Perspective. *Psychological Science*, *16*(4), 255-259.

Lubyk, D. M., Dupuis, b., Gutierrez, L., & Spetch, M. L. (2012). Geometric orientation by humans: Angles weigh in. *Psychological Bulletinand Review, 19,* 436-442.

Mackintosh, N. J. (1975). A theory of attention: Variations in associability of stimuli with reinforcement. *Psychological Review, 82*(4), 276-298.

Mackintosh, N. J. (1976). Overshadowing and stimulus-intensity. *Animal Learning and Behavior, 4*(2), 186-192.

Mackintosh, N. J., & Little, L. (1969). Intradimensional and extradimensional shift learning by pigeons. *Psychonomic Science, 14*(1), 5-6.

Margules, J., & Gallistel, C. R. (1988). Heading in the rat: Determination by environmental shape. *Animal Learning and Behavior, 16*(4), 404-410.

McGregor, A., Horne, M. R., Esber, G. R., & 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*(3), 357-370.

McGregor, A., Jones, P. M., Good, M. A., & Pearce, J. M. (2006). Further evidence that rats rely on local rather than global spatial information to locate a hidden goal: Reply to Cheng and Gallistel (2005). *Journal of Experimental Psychology: Animal Behavior Processes, 32*(3), 314-321.

Miles, C. G., & Jenkins, H. M. (1973). Overshadowing in operant conditioning as a function of discriminability. *Learning and motivation, 4*(1), 11-27.

Miller, N. Y., & Shettleworth, S. J. (2007). Learning about environmental geometry: An associative model. *Journal of Experimental Psychology: Animal Behavior Processes, 33*(3), 191-212.

Miller, N. Y., & Shettleworth, S. J. (2008). An associative model of geometry learning: A modified choice rule. *Journal of Experimental Psychology: Animal Behavior Processes, 34*(3), 419-422.

Miller, N. Y., & Shettleworth, S. J. (2013). Associative models of instrumental learning: A response to Dupuis and Dawson. *Journal of Experimental Psychology: Animal Behavior Processes, 39*(3), 287-293.

Morgan, C. L. (1894). *An Introduction to Comparative Psychology*. London, UK: Walter Scott

Mueller, S. C., Jackson, C. P. T., & Skelton, R. W. (2008). Sex differences in a virtual water maze: An eye tracking and pupillometry study. *Behavioural Brain Research, 193*(2), 209-215.

Nardi, D., & Bingman, V. P. (2009). Pigeon (Columba livia) Encoding of a Goal Location: The Relative Importance of Shape Geometry and Slope Information. *Journal of Comparative Psychology, 123*(2), 204-216.

Nardi, D., Newcombe, N. S., & Shipley, T. F. (2011). The World Is Not Flat: Can People Reorient Using Slope? *Journal of Experimental Psychology: Learning Memory and Cognition, 37*(2), 354-367.

Nardi, D., Nitsch, K. P., & Bingman, V. P. (2010). Slope-Driven Goal Location Behavior in Pigeons. *Journal of Experimental Psychology: Animal Behavior Processes, 36*(4), 430-442.

Nardini, M., Jones, P., Bedford, R., & Braddick, O. (2008). Development of cue integration in human navigation. *Current Biology, 18*(9), 689-693.

Newcombe, N. S., Ratliff, K. R., Shallcross, W. L., & Twyman, A. D. (2010). Young children's use of features to reorient is more than just associative: further evidence against a modular view of spatial processing. *Developmental Science, 13*(1), 213-220.

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

Pavlov, I. P. (1927). *Conditioned reflexes* (G. V. Anrep, Trans.). London: Oxford University Press.

Pearce, J. M. (1987). A model for stimulus-generalization in pavlovian conditioning. *Psychological Review, 94*(1), 61-73.

Pearce, J. M. (2009). The 36th Sir Frederick Bartlett Lecture: An associative analysis of spatial learning. *Quarterly Journal of Experimental Psychology, 62*(9), 1665-1684.

Pearce, J. M., Esber, G. P., George, D. N., & Haselgrove, M. (2008). The nature of discrimination learning in pigeons. *Learning and Behavior, 36*(3), 188-199.

Pearce, J. M., Good, M. A., Jones, P. M., & McGregor, A. (2004). Transfer of spatial behavior between different environments: Implications for theories of spatial learning and for the role of the hippocampus in spatial learning. *Journal of Experimental Psychology: Animal Behavior Processes, 30*(2), 135-147.

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*(3), 201-214.

Pearce, J. M., & Hall, G. (1980). A model for pavlovian learning: Variations in the effectiveness of conditioned but not of unconditioned stimuli. *Psychological Review, 87*(6), 532-552.

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*(4), 329-344.

Peirce, J. W. (2007). PsychoPy - Psychophysics software in Python. *Journal of Neuroscience Methods, 162*(1-2), 8-13.

Poulter, S. L., Kosaki, Y., Easton, A., & McGregor, A. (2013). Spontaneous object recognition memory is maintained following transformation of global geometric properties. *Journal of Experimental Psychology: Animal Behavior Processes, 39*(1), 93-98.

Prados, J., Redhead, E. S., & Pearce, J. M. (1999). Active preexposure enhances attention to the landmarks surrounding a Morris swimming pool. *Journal of Experimental Psychology: Animal Behavior Processes, 25*(4), 451-460.

Ratliff, K. R., & Newcombe, N. S. (2008a). Reorienting When Cues Conflict: Evidence for an Adaptive-Combination View. *Psychological Science, 19*(12), 1301-1307.

Ratliff, K. R., & Newcombe, N. S. (2008b). Is language necessary for human spatial reorientation? Reconsidering evidence from dual task paradigms. *Cognitive Psychology, 56*(2), 142-163.

Redhead, E. S., & Hamilton, D. A. (2007). Interaction between locale and taxon strategies in human spatial learning. *Learning and Motivation, 38*(3), 262-283.

Redhead, E. S., & Hamilton, D. A. (2009). Evidence of blocking with geometric cues in a virtual watermaze. *Learning and Motivation, 40*(1), 15-34.

Redhead, E. S., Hamilton, D. A., Parker, M. O., Chan, W., & Allison, C. (2013). Overshadowing of geometric cues by a beacon in a spatial navigation task. *Learning and Behavior, 41*(2), 179-191.

Redhead, E. S., Prados, J., & Pearce, J. M. (2001). The effects of pre-exposure on escape from a Morris pool. *Quarterly Journal of Experimental*

Psychology Section B: Comparative and Physiological Psychology, 54(4), 353-367.

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*(3), 340-350.

Rescorla, R. A. (1971). Variation in the effectiveness of reinforcement and nonreinforcement following prior inhibitory conditioning. *Learning and Motivation, 2*(2), 113-123.

Rescorla, R. A., & Wagner, A. R. (1972). A theory of Pavlovian conditioning: Variations in the effectiveness of reinforcement and non-reinforcement. In A. H. Black & W. F. Prokasy (Eds.), *Classical conditioning II: Current research and theory.* (pp. 64 - 99). New York Appleton-Century-Crofts.

Rhodes, S. E. V., Creighton, G., Killcross, A. S., Good, M., & Honey, R. C. (2009). Integration of geomtric with luminance informaiotn in the rat: Evidence from within-compound assocaitions. *Journal of Experimental Psychology: Animal Behavior Processes, 35*(1), 92-98.

Roberts, A. C., Robbins, T. W., & Everitt, B. J. (1988). The effects of intradimensional and extradimensional shifts on visual-discrimination learning in humans and non-human primates. *Quarterly Journal of Experimental Psychology Section B: Comparative and Physiological Psychology, 40*(4), 321-341.

Roberts, A. D. L., & Pearce, J. M. (1999). Blocking in the Morris swimming pool. *Journal of Experimental Psychology: Animal Behavior Processes, 25*(2), 225-235.

Rock, I., Wheeler, D., & Tudor, L. (1989). Can we imagine how objects look from other viewpoints. *Cognitive Psychology, 21*(2), 185-210.

Rodrigo, T., Arall, M., & Chamizo, V. D. (2005). Blocking and unblocking in a navigation task. *Psicológica, 26*(2), 229-241.

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*(1), 110-118.

Sanchez-Moreno, J., Rodrigo, T., Chamizo, V. D., & MacKintosh, N. J. (1999). Overshadowing in the spatial domain. *Animal Learning and Behavior, 27*(4), 391-398.

Save, E., & Poucet, B. (2000). Involvement of the hippocampus and associative parietal cortex in the use of proximal and distal landmarks for navigation. *Behavioural Brain Research, 109*(2), 195-206.

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*(2), B51-B59.

Sovrano, V. A., Bisazza, A., & Vallortigara, G. (2003). Modularity as a fish (Xenotoca eiseni) views it: Conjoining geometric and nongeometric information for spatial reorientation. *Journal of Experimental Psychology: Animal Behavior Processes, 29*(3), 199-210.

Spelke, E. S., & Lee, S. A. (2012). Core systems of geometry in animal minds. *Royal Society Philosophical Transactions Biological Sciences, 367*(1603), 2784-2793.

Spence, K. W. (1940). Continuous versus non-continuous interpretations of discrimination learning. *Psychological Review, 47*, 271-288.

Spence, K. W. (1952). The nature of the response in discrimination learning. *Psychological Review, 59*(1), 89-93.

Stahlman, W. D., & Blaisdell, A. P. (2009). Blocking of spatial control by landmarks in rats. *Behavioural Processes, 81*(1), 114-118.

Stuerzl, W., Cheung, A., Cheng, K., & Zeil, J. (2008). The information content of panoramic images I: The rotational errors and the similarity of views in rectangular experimental arenas. *Journal of Experimental Psychology: Animal Behavior Processes, 34*(1), 1-14.

Sturz, B. R., & Bodily, K. D. (2011). Is surface-based orientation influenced by a proportional relationship of shape parameters? *Psychonomic Bulletin and Review, 18*(5), 848-854.

Sturz, B. R., Forloines, M. R., & Bodily, K. D. (2012). Enclosure size and the use of local and global geometric cues for reorientation. *Psychonomic Bulletin and Review, 19*(2), 270-276.

Sturz, B. R., Gurley, T., & Bodily, K. D. (2011). Orientation in Trapezoid-Shaped Enclosures: Implications for Theoretical Accounts of Geometry Learning. *Journal of Experimental Psychology: Animal Behavior Processes, 37*(2), 246-253.

Sturz, B. R., Kilday, Z. A., & Bodily, K. D. (2013). Does constraining field of view prevent extraction of geometric cues for humans during virtual-environment reorientation? *Journal of Experimental Psychology: Animal Behavior Processes, 39*(4), 390.

Sutton, J. E., Joanisse, M. F., & Newcombe, N. S. (2010). Spinning in the Scanner: Neural Correlates of Virtual Reorientation. *Journal of Experimental Psychology: Learning Memory and Cognition, 36*(5), 1097-1107.

Tolman, E. C. (1948). Cognitive maps in rats and men. *Psychological Review, 55*(4), 189-208.

Tolman, E. C., Ritchie, B. F., & Kalish, D. (1946). Studies in spatial learning. I. Orientation and the short-cut. *Journal of Experimental Psychology, 36*(1), 13-24.

Tommasi, L., Chiandetti, C., Pecchia, T., Sovrano, V. A., & Vallortigara, G. (2012). From natural geometry to spatial cognition. *Neuroscience and Biobehavioral Reviews, 36*(2), 799-824.

Tommasi, L., & Polli, C. (2004). Representation of two geometric features of the environment in the domestic chick (Gallus gallus). *Animal Cognition, 7*(1), 53-59.

Trobalon, J. B., Miguelez, D., McLaren, I. P. L., & Mackintosh, N. J. (2003). Intradimensional and extradimensional shifts in spatial learning. *Journal of Experimental Psychology: Animal Behavior Processes, 29*(2), 143-152.

Tversky, B., Kim, J., & Cohen, A. (1999). Mental models of spatial relations and transformations from language. *Advances in psychology, 128*, 239-258.

Twyman, A., Friedman, A., & Spetch, M. L. (2007). Penetrating the geometric module: Catalyzing children's use of landmarks. *Developmental Psychology, 43*(6), 1523-1530.

Twyman, A. D., & Newcombe, N. S. (2010). Five Reasons to Doubt the Existence of a Geometric Module. *Cognitive Science, 34*(7), 1315-1356.

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*(3), 248-254.

Vargas, J. P., López, J. C., Salas, C., & Thinus-Blanc, C. (2004). Encoding of Geometric and Featural Spatial Information by Goldfish (Carassius auratus). *Journal of Comparative Psychology, 118*(2), 206-216.

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*(3), 289-298.

Wallace, D. G., Hines, D. J., Pellis, S. M., & Whishaw, I. Q. (2002). Vestibular information is required for dead reckoning in the rat. *Journal of Neuroscience, 22*(22), 10009-10017.

Wang, R. F., Hermer, L., & Spelke, E. S. (1999). Mechanisms of reorientation and object localization by children: A comparison with rats. *Behavioral Neuroscience, 113*(3), 475-485.

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. Jeffery (Ed.), *The Neurobiology of Spatial Behavior* (pp. 119 - 143). Oxford, UK: Oxford University Press.

Williams, B. A., & McDevitt, M. A. (2002). Inhibition and superconditioning. *Psychological Science, 13*(5), 454-459.

Wilson, P. N., & Alexander, T. (2008). Blocking of Spatial Learning Between Enclosure Geometry and a Local Landmark. *Journal of Experimental Psychology: Learning Memory and Cognition, 34*(6), 1369-1376.

Wilson, P. N., & Alexander, T. (2010). Enclosure shape influences cue competition effects and goal location learning. *Quarterly Journal of Experimental Psychology, 63*(8), 1552-1567.

Zacks, J. M., Vettel, J. M., & Michelon, P. (2003). Imagined viewer and object rotations dissociated with event-related fMRI. *Journal of Cognitive Neuroscience, 15*(7), 1002-1018.