Cue interaction during reorientation of human adults

by

Lin Wang

A thesis submitted in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

Department of Psychology University of Alberta

© Lin Wang, 2018

#### Abstract

Reorientation is an important behavior for humans and non-human animals in everyday life. To determine one's orientation, navigators could use various cues in the environment. Studies on competition and combination of multiple cues are quite diverse. In this dissertation, I first introduced three types of cue interactions and the methods to investigate them. Secondly, I reviewed the most important findings of cues interaction in reorientation and factors that influence the interaction. Then I discussed several theories and their interpretation of the interaction among the cues. Finally, I reported two studies investigating human adults' use of multiple cues during orientation. Overall, I provided evidence that cue interaction during reorientation is affected by enclosure size and navigator's familiarity with the environment.

#### Preface

This thesis is an original work by Lin Wang. The research project, of which this thesis is a part, received research ethics approval from the University of Alberta Research Ethics Board, Project Name "Human spatial cognition", No. Pro00052545, November 20, 2014.

Chapter 2 of the thesis has been published as "Wang, L., Mou, W., & Dixon, P. (2018). Cue interaction between buildings and street configurations during reorientation in familiar and unfamiliar outdoor environments. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 44*(4), 631-644." I was responsible for the data collection and analysis as well as the manuscript composition. W. Mou was involved with concept formation and manuscript composition. P. Dixon was involved with data analysis and manuscript composition.

#### Acknowledgments

First and foremost, I would like to express my sincere gratitude to my supervisor, Dr. Weimin Mou. Without your guidance and support, this work would not have been possible. Your insight and rigorousness in research, and your patience and devotion to the students will always guide me through my career path as a scientific researcher. I will never forget your help to me and my family both as a supervisor and as a friend.

I would like to thank my PhD supervisory committee, which consisted of Drs. Jeremy Caplan and Peter Dixon. I am especially grateful for all your valuable feedback and support along the way. I would also like to thank the additional members of my PhD examination committee, including Drs. Norman Brown, Craig Chapman, Debbie Kelly. Your thoughtful comments on my dissertation and questions during my defence were greatly appreciated.

I would like to thank all my labmates in the Virtual Reality and Spatial Cognition Lab, Karen Du, Xuehui Lei, Ruojing Zhou and Lei Zhang. Thank you for helping me prepare my defense and your thoughtful comments on my work. I would also like to thank the research assistants who helped me collecting the data. Aleesha Amjad Hafeez, Bairong Song, Silvernise Goh, Xinyu Yi, thank you for your time and effort in assisting my work.

I would like to thank all the staffs in the general office in the department of psychology for your assistance. Additionally, I would also like to thank the various funding agencies that financially supported the work I report in my dissertation, namely the National Science and Engineering Council of Canada (NSERC), and the University of Alberta.

Finally, I would like to thank my family, specifically my parents, Yunhua Wang and Hongyu Yang, my grandparents, Xintian Wang and Jiuru Xiao, my husband, Shang Lu, and his parents, Ling Xu and Jiyong Lu. Without your love and support, obtaining my PhD would have been impossible. I would like to give special thanks to my daughter Summer Lu and my son Sunny Lu. You have made my life beautiful and complete.

Sincerely,

Lin Wang, PhD

April 30, 2018

# Table of Contents

Chapter 1	1 Introduction	1
1.1	Background	2
1.2	Cue types and interaction	4
1.2.1	1 Competition during encoding	7
1.2.2	2 Combination during retrieval	9
1.2.3	3 Competition during retrieval	9
1.3	Factors that affect cue interaction in reorientation	14
1.3.1	1 The effect of room size	15
1.3.2	2 The effect of experience	18
1.4	Theories of cue interaction in reorientation	20
1.4.1	1 The modularity theories	21
1.4.2	2 The unified theories	24
1.5	Goal of current work	27
1.6	References	30
Chapter 2	2 Cue Interaction between Buildings and Street Configurations during Reorie	ntation in
Familiar a	and Unfamiliar Outdoor Environments	41
Familiar a 2.1	and Unfamiliar Outdoor Environments	<b> 41</b> 42
Familiar a 2.1 2.2	and Unfamiliar Outdoor Environments Abstract Introduction	<b>41</b> 42 44
Familiar a 2.1 2.2 2.3	Abstract	<b>41</b> 42 44 53
Familiar a 2.1 2.2 2.3 2.3.1	Abstract	
Familiar a 2.1 2.2 2.3 2.3.1 2.3.2	Abstract Abstract Introduction General Method Materials and Design Procedure	
Familiar a 2.1 2.2 2.3 2.3.1 2.3.2 2.3.3	and Unfamiliar Outdoor Environments   Abstract   Introduction   General Method   1 Materials and Design   2 Procedure   3 Competition during Encoding	
Familiar a 2.1 2.2 2.3 2.3.1 2.3.2 2.3.3 2.3.4	and Unfamiliar Outdoor Environments	
Familiar a 2.1 2.2 2.3 2.3.1 2.3.2 2.3.3 2.3.4 2.3.5	and Unfamiliar Outdoor Environments	
Familiar a 2.1 2.2 2.3 2.3.1 2.3.2 2.3.3 2.3.4 2.3.5 2.4	And Unfamiliar Outdoor Environments	
Familiar a 2.1 2.2 2.3 2.3.1 2.3.2 2.3.3 2.3.4 2.3.5 2.4 2.4.1	And Unfamiliar Outdoor Environments.   Abstract   Introduction   General Method   1 Materials and Design   2 Procedure   3 Competition during Encoding   4 Combination during Retrieval   5 Competition during Retrieval   6 Longettion during Retrieval   1 Method	
Familiar a 2.1 2.2 2.3 2.3.1 2.3.2 2.3.3 2.3.4 2.3.5 2.4 2.4.1 2.4.2	and Unfamiliar Outdoor Environments   Abstract   Introduction   General Method   1 Materials and Design   2 Procedure   3 Competition during Encoding   4 Combination during Retrieval   5 Competition during Retrieval   6 Longetition during Retrieval   7 Method   1 Method   2 Results and Discussion	
Familiar a 2.1 2.2 2.3 2.3.1 2.3.2 2.3.3 2.3.4 2.3.5 2.4 2.4.1 2.4.2 2.5	and Unfamiliar Outdoor Environments   Abstract   Introduction   General Method   1 Materials and Design   2 Procedure   3 Competition during Encoding   4 Combination during Retrieval   5 Competition during Retrieval   6 Lamperiment 1   1 Method   2 Results and Discussion   Experiment 2 Experiment 2	
Familiar a 2.1 2.2 2.3 2.3.1 2.3.2 2.3.3 2.3.4 2.3.5 2.4 2.4.1 2.4.2 2.5 2.5 2.5.1	and Unfamiliar Outdoor Environments   Abstract   Introduction   General Method   1 Materials and Design   2 Procedure   3 Competition during Encoding   4 Combination during Retrieval   5 Competition during Retrieval   6 Lambda and Discussion   1 Method   2 Results and Discussion   1 Method   2 Results and Discussion	
Familiar a 2.1 2.2 2.3 2.3.1 2.3.2 2.3.3 2.3.4 2.3.5 2.4 2.4.1 2.4.2 2.5 2.5 2.5.1 2.5.1	and Unfamiliar Outdoor Environments   Abstract   Introduction   General Method   1 Materials and Design   2 Procedure   3 Competition during Encoding   4 Combination during Retrieval   5 Competition during Retrieval   6 Competition during Retrieval   7 Method   8 Results and Discussion   6 Experiment 2   1 Method   2 Results and Discussion	

2.6	General Discussion75
2.7	Appendix
2.8	References
Chapter 3	Effects of Familiarity and Room Size on the Interaction between Geometry and Features
during Re	orientation
3.1	Abstract
3.2	Introduction
3.3	General method
3.3.1	Materials and Design
3.3.2	Procedure
3.3.3	Data Analysis
3.4	Experiment 1
3.4.1	Method
3.4.2	Results and Discussion
3.5	Experiment 2
3.5.1	Method
3.5.2	Results and Discussion
3.6	Experiment 3126
3.6.1	Method
3.6.2	Results and Discussion127
3.7	General Discussion
3.8	References
Chapter 4	General Discussion
4.1	Review of Experiments142
4.2	Novel Findings and Implications144
4.2.1	Familiarity affects cue interaction144
4.2.2	Room size affects the relative use of cues by modulating cue stability but not salience146
4.2.3	2D patterns and isolated objects interact differently with room geometry148
4.2.4	Implications and future directions150
4.3	References153
Bibliogra	ohy156

List of Tables

*Table 1. Observed mean accuracy as a function of testing cue type (S, B, SB) and competition group with and without removing the first trial in each testing cue type.* 

Table 2. Observed mean accuracy in single cue and both cues condition, and mean cue preference in the conflict cue condition in Du et al. (2016), and the predictions in the both cues and conflict cues conditions based on the accuracy-based combination model developed in the current study (Equations 2 and 4).

List of Figures

Figure 1.1. Illustration of the conflict paradigm in reorientation studies. Participants learn a target at one corner (denoted by X) with respect to the room geometry and a feature (e.g. a blue wall). At test, the feature is displaced relative to the room. The participants are forced to choose among the geometrically correct corners, the featurally correct corner and the incorrect corner.

Figure 1.2. Illustration of salience of room geometry in small and large rooms. Sovrano and Vallortigara (2006) proposed that geometric information, such as the lengths of the walls, is more easily observed in a smaller enclosure. When at a certain distance from a corner, a navigator could see a larger proportion of the room in a small room than in a large room. Figure 2.1. An example of the experimental environments (bird's eye view).

Figure 2.2. Examples of the experimental conditions of Experiments 1 and 2.  $\otimes$  denotes the building. Four objects were located at the end of the four streets respectively. X denotes the original location of one target object. At learning, participants were transported to each object at a constant speed by the computer. At testing, participants were released at the center of the intersection and were asked to choose between the two streets denoted by X and Y. X and Y had the same length. When four streets had the same lengths during testing in the B-test-trials, X and Y had the same angular distance from the building, i.e., both closer to the building or both farther away from the building.

Figure 2.3. Proportion correct in locating target objects as a function of testing cue type and learning cue group in Experiment 1. Error bars represent standard errors of the mean.

Figure 2.4. Observed and estimated proportion correct in locating target objects when both buildings and street configurations indicated the same orientation ( $A_{SB}$ ) in the competition group in Experiment 1. Error bars represent standard errors of the mean.

Figure 2.5. The observed and estimated percentage of choosing the response location indicated by the street configuration when the building and the street configuration were in conflict ( $P_{S|Conflict}$ ) in the competition group in Experiment 1. Error bars represent standard errors of the mean.

Figure 2.6. Proportion correct in locating target objects as a function of testing cue type and learning cue group in Experiment 2. Error bars represent standard errors of the mean. Figure 2.7. Observed and estimated proportion correct in locating target objects when both buildings and street configurations were presented (A<sub>SB</sub>) in the competition group in Experiment 2. Error bars represent standard errors of the mean.

Figure 2.8. The observed and estimated percentage of choosing the response location indicated by the street configuration when the building and the street configuration were in conflict ( $P_{S|Conflict}$ ) in the competition group in Experiment 2. Error bars represent standard errors of the mean.

Figure 3.1. Examples of the within-subject conditions in all the experiments. In Experiment 1 and 2, the features were two identical cuing objects placed in front of two opposite walls, as denoted by the red dots. In Experiment 3, the features were two identical shape on two opposite walls as denoted by the blue bars. Four target objects were located at the four corners respectively. X denotes the location or the equivalent location for one target object.

Figure 3.2. Three hypothesized results of the experiment. a) If the difference between the cue preferences in the small room and in the large room is comparable to the difference between the relative salience in the small room and in the large room, the room size effect on cue preference can be fully explained by the room size effect on relative salience during encoding. b) If room size affects the cue preference but does not affect the relative salience, the room size effect on cue preference should be attributed to the room size effect on cue weighting during retrieval. c) If room size affects both the cue preference and the relative salience, but the difference between the cue preferences in the small room and in the large room is different from the difference between the relative salience in the small room and in the large room, the room size effect on cue preference should be attributed to the room size effect or cue weighting during retrieval. c) If room size affects both the cue preference and the relative salience, but the difference between the cue preferences in the small room and in the large room is different from the difference between the relative salience in the small room and in the large room, the room size effect on cue preference should be attributed to the room size effect on the room size effect on both relative salience during encoding and cue weighting during retrieval. Figure 3.3. Proportion correct in locating target objects as a function of testing cue type and room size in Experiment 1. Error bars represent standard errors of the mean. Figure 3.4. The observed and estimated percentage of choosing the response location

indicated by the room shape when the room shape and the cuing objects were in conflict  $(P_{G|Conflict})$  as a function of room size in Experiment 1. Error bars represent standard errors of the mean.

Figure 3.5. Observed and estimated proportion correct in locating target objects when both room shape and cuing objects indicated the same orientation ( $A_{GF}$ ) as a function of room size in Experiment 1. Error bars represent standard errors of the mean.

Figure 3.6. Proportion correct in locating target objects as a function of testing cue type and room size in Experiment 2. Error bars represent standard errors of the mean.

Figure 3.7. The observed and estimated percentage of choosing the response location indicated by the room shape when the room shape and the cuing objects were in conflict  $(P_{G|Conflict})$  as a function of room size in Experiment 2. Error bars represent standard errors of the mean.

Figure 3.8. Observed and estimated proportion correct in locating target objects when both room shape and cuing objects indicated the same orientation ( $A_{GF}$ ) as a function of room size in Experiment 2. Error bars represent standard errors of the mean.

Figure 3.9. Proportion of choosing the correct corners as a function of testing cue type and room size in Experiment 3. Error bars represent standard errors of the mean.

Figure 3.10. The observed and estimated percentage of choosing the corners indicated by the room shape when the room shape and the wall features were in conflict ( $P_{G|Conflict}$ ) as a function of room size in Experiment 3. Error bars represent standard errors of the mean. Figure 3.11. Observed and estimated proportion of choosing the correct corners when both room shape and wall features indicated the same orientation ( $A_{GF}$ ) as a function of room size

in Experiment 3. Error bars represent standard errors of the mean.

# Chapter 1 Introduction

What would you do if you lost your way in the wild? Navigators may try to retrieve their orientation based on the direction of the sun or a huge mountain or keep track of their orientation using a big tree, or they may determine their orientation using all the cues in the environment. For decades, scientists have been interested in what kinds of cues are used to retrieve one's orientation and how these cues interact with each other.

Studies on cue interaction have focused on three questions. First, whether learning one cue affects learning another cue. Second, whether using multiple cues are better than using one cue. Third, which cue is preferred when the cues are in conflict. In previous studies, scientists found that cue interaction during reorientation is determined by the properties of the cues, the environment, as well as the experience of the navigators. The aim of the current dissertation is to investigate cue interaction during reorientation of human adults and how different factors modulate cue interaction.

#### 1.1 Background

The most influential study in reorientation was conducted by Cheng. In 1986, Cheng tested how rats retrieve their orientation in a rectangular room with four distinctive patterned panels and walls of different colors. The rats were trained to locate food hidden at one of the corners of the room and the location of the food varied across trials. Cheng found that rats could only use room shape, but not panels with different patterns or wall colors to identify the corners of a room. He proposed a geometric module theory that the shape of the room is a geometric cue and is processed with a geometric module, whereas the panels and wall colors are featural cues that are only learned associatively. Since then, this theory has raised controversy for decades. The advocates support that geometry and features are two types of cues that are processed within different regions of the brain, whereas the opponents claim that there is no fundamental difference between geometry and features, therefore such a distinction may not be necessary.

Both groups of researchers provided empirical evidence to support or oppose the geometric module theory. Researchers who support the geometric module theory provided evidence that rats and human children can only use geometric cues but not featural cues (Cheng, 1986; Hermer & Spelke, 1994, 1996) and geometric cues cannot be overshadowed or blocked by featural cues (Pearce, Ward-Robinson, Good, Fussell, & Aydin, 2001; Sovrano, Bisazza, & Vallortigara, 2003; Wall, Botly, Black, & Shettleworth, 2004). However, other researchers argued that a processing module is not necessary to interpret those findings. Moreover, they suggested that geometry is not always dominant by showing that features could overshadow geometry (Gray, Bloomfield, Ferrey, Spetch, & Sturdy, 2005; Pearce, Graham, Good, Jones, & McGregor, 2006) and was preferred over geometry under certain conditions (Ratliff & Newcombe, 2008; Sovrano, Bisazza, & Vallortigara, 2005, 2007).

In the following sections of the introduction, I will discuss previous studies in detail. Firstly, I will introduce the definition of features and geometry and the methods to investigate cue interaction. Secondly, I will review the most important findings of cue interaction in reorientation and the factors that affect cue interaction. Thirdly, I will introduce two groups of theories and how they interpret interaction between geometry and features during reorientation. Finally, I will propose a new method to systematically examine cue interaction in reorientation.

#### 1.2 Cue types and interaction

In the literature of reorientation, the discussion mostly focused on two types of cues: geometric cues and featural cues. To understand the long-lasting debate in this area, we need to first understand the definition of features and geometry and how they assist navigators to identify their orientation. Cheng (1986) first proposed the distinction between geometry and features. In his experiments, he used patterned panels and colors of walls as featural cues and room shape as the geometric cue. Although he found that the rats responded differently to those two types of cues, he did not give a clear definition of each cue. Based on Cheng's research, Gallistel (1990) differentiated geometric properties from non-geometric features. A geometric property of a stimulus is its "position relative to other stimuli", whereas a nongeometric feature of a stimulus is "any property that cannot be described as relative position alone, such as color, luminance, texture and so on" (pp. 212).

According to Gallistel's definition, geometry could be the shape of walls forming an enclosure, the configuration of isolated objects or the shape of a tabletop arena (Gouteux, Vauclair, & Thinus-Blanc, 2001). However, to understand why navigators respond differently to geometry and features, Lee and Spelke (2010a) further restricted the definition. They defined features as either 2D shapes or isolated objects and geometry as the shape of extended surfaces. This definition is supported by findings that young children could reorient using the shape of walls or other 3D boundaries but not the configuration of object arrays or 2D shapes (Gouteux & Spelke, 2001; Lee & Spelke, 2011).

In the first study of reorientation, Cheng (1986) used four panels of different patterns and colors of walls as featural cues. Since then, researchers have used patterned panels,

doors, distinctive objects, curtains, colors of walls as featural cues (for reviews, see Cheng & Newcombe, 2005; Twyman & Newcombe, 2010; Vallortigara, 2009). Features can be used as beacons or associative cues in reorientation, depending on their relationship with the target. When using a feature as a beacon, navigators can reach their destination by simply approaching or avoiding the feature. It usually happens when the feature is located close to the target location, in which case navigators only need to approach the feature. Another situation of using a feature as a beacon is that when there are two choices in the environment, navigators have to remember whether to move towards or away from the feature. In both cases, navigators do not need to encode metric information. However, when the target is at a certain distance or direction from a feature, navigators have to use the feature as an associative cue, i.e., associate the feature with an action. For example, if the navigators memorize a location as "500 m north" of an object, they are using the object as an associative cue. Studies with human adults have shown that learning features as beacons is faster than as associative cues (Waller & Lippa, 2007; Wang, Mou & Sun, 2014). In addition, studies have shown that young children at 4 years old can use features as beacons but not as associative cues in reorientation (Learmonth et al., 2008).

In previous studies, geometric cues were mostly the shapes of the experimental rooms. In most of those experiments, two long walls and two short walls defined a rectangular area, making two of the corners (a short wall on the left and a long wall on the right) different from the other two (a long wall on the left and a short wall on the right). Other studies also used trapezium, rhombic, octagon, parallelogram- and kite-shaped rooms as geometric cues (Bodily, Eastman, & Sturz, 2011; Buckley, Smith, & Haselgrove, 2016; Hupbach & Nadel,

2005; Lubyk, Dupuis, Gutierrez, & Spetch, 2012; Newcombe, Ratliff, Shallcross & Twyman, 2010).

Theoretically, geometric properties of a room consist of the relative lengths, heights, angles and distances of the walls. However, research shows that the essence of geometric cues is the distance and directional relations among extended surfaces. Lee, Sovrano and Spelke (2012) found that 2-year-old children could reorient themselves using four detached walls of the same length forming a rectangle area but could not do so using four detached walls of different lengths forming a square area. Similarly, young children could reorient themselves in a rhombic room but could not do so using only the angular information of the corners when the walls connecting the corners were removed (Lee, Sovrano & Spelke, 2012). Other researchers suggested that angles between walls function like features rather than geometry because they only provide local information but not global shapes (Kelly, Chiandetti, & Vallortigara, 2011; Sturz, Forloines, & Bodily, 2012).

Recently, researchers have been interested in the role of vertical cues in reorientation. Nardi, Newcombe and Shipley (2011) found human adults could use vertical heights to reorient in a room with a tilted floor. Hu and colleagues (2015) tested reorientation of children in a room with a tilted ceiling and found that children could not use the height information as early as other geometric properties such as distance. They explained that height is less important than horizontal distance because humans are limited in the plane of horizon, and could not freely move in the vertical dimension. Du, Spetch and Mou (2016) tested how human adults use wall heights and room shapes during reorientation and did not find the room shape to be predominant. More surprisingly, Du and colleagues (2016) found

that pigeons, which move remarkably in the vertical dimension, preferred the horizontal geometries over the vertical heights. So far, the role of height in the taxonomy of geometry and features is not clear. In this dissertation, I will mainly focus on geometry as the distance and directional relations among extended surfaces, and features as 2D shapes and isolated objects, as defined by Lee and Spelke (2010a).

The interaction effect between featural and geometric cues has been a core topic in spatial reorientation. Cue interaction during spatial navigation could be categorized into three types. First, how two cues compete during encoding. Second, how two cues are combined during retrieval. Third, how two cues compete during retrieval.

# **1.2.1** Competition during encoding

Competition of cues during encoding can be examined using the overshadowing or blocking paradigm. The overshadowing effect means the learning of one cue will interfere with the learning of another cue that is presented simultaneously (Pavlov, 1927). For example, if cue A overshadows cue B, the performance when people are trained with both cue A and cue B and are tested with cue B will be worse than the performance when they are trained and tested with only cue B. The blocking effect means the experience of learning one cue will interfere with the learning of another cue that is presented later (Kamin, 1969). For example, the participants learn to associate a target with cue A, next they learn to associate the target with both cue A and cue B, finally they are tested with cue B alone. If cue A blocks cue B, the performance would be worse than if they learn the target with cue A and cue B without any experience of learning cue A and are tested with cue B alone.

Studies examining overshadowing and blocking effects between features and geometry

show diverse results. Doeller and Burgess (2008) found that, during goal localization of human adults, learning a 3D circular boundary overshadowed learning an isolated landmark but not vice versa. However, Wilson and Alexander (2008) found learning an irregular-shaped enclosure and learning a landmark blocked each other, although the blocking effect was much stronger when the enclosure was the blocking cue. Research on fish showed that learning landmarks as beacons overshadowed learning landmarks as associative cues, but did not overshadow learning a geometric cue (Sovrano, Bisazza, & Vallortigara, 2003). Research on rats showed that learning a beacon did not block or overshadow learning the shape of a room (Hayward, Good, & Pearce, 2004; Hayward, McGregor, Good, & Pearce, 2003; Pearce, Ward- Robinson, Good, Fussell, & Aydin, 2001; Wall, Botly, Black, & Shettleworth, 2004). Those studies suggest that geometry is more dominant during the encoding phase of reorientation.

However, learning a colored wall overshadowed learning the shape of a room during the reorientation of rats (Pearce, Graham, Good, Jones, & McGregor, 2006) and wild-caught mountain chickadees (Poecile gambeli) (Gray, Bloomfield, Ferrey, Spetch, & Sturdy, 2005). The overshadowing effect is also affected by room size. Chicks learned the location of food with respect to four distinctive patterned panels in a rectangular room. At test, if the panels were removed, chicks were more likely to correctly use the geometric cue in a small room than in a large room. If the rectangular room was shifted to a square room, chicks were more likely to correctly use the featural cue in a large room than in a small room (Chiandetti, Regolin, Sovrano, & Vallortigara, 2007).

# **1.2.2** Combination during retrieval

When two cues are presented, whether the navigator will only use the dominant cue, alternatively use two or more cues, or combine the cues attracted many researchers. Combining multiple cues is advantageous because it produces better performance by reducing the variance of estimations. Bayes' (1763) theorem claims that the optimal combination happens when the weights of the cues are proportional to the inverse of its variance, that is, the more reliable cue is assigned more weight. The combination of spatial information from multiple sources has been tested in diverse species (see Cheng, Shettleworth, Huttenlocher, & Rieser, 2007 for a review). Researchers found that, when localizing a target, human adults could combine landmark cues and self-motion cues optimally based on Bayesian principles so that the variance of their estimation was minimized, whereas human children could not integrate the cues to reduce response variance, and instead, they alternatively chose between the two cues (Nardini, Jones, Bedford, & Braddick, 2008). However, cue combination is rarely tested in the field of reorientation. Most combination models are based on variance reduction, whereas most reorientation studies dealt with the probability of choosing a corner by all the participants, in which variance is hard to obtain.

# **1.2.3** Competition during retrieval

A special case of cue combination during retrieval is combining two cues when they are in conflict. When the two cues are consistent with each other, it is advantageous to combine the cues together. However, if the two cues are in conflict, combining the two cues may not be a good solution. Previous studies have shown that whether participants combine

conflicting cues depends on the discrepancy between the cues. If the discrepancy is small, participants still judge the two cues are from the same source and thus combine them; whereas if the discrepancy is large, participants will judge the two cues are from different sources and thus do not combine them (Cheng, Shettleworth, Huttenlocher, & Rieser, 2007). In the former case, the response is a weighted average of the estimated locations based on the two cues; in the latter case, the response is determined by the more weighted cue in a winner-take-all fashion. Moreover, the weights assigned to the cues are determined through different mechanisms when the discrepancy is small or large. Cheng and colleagues (2007) proposed that, when the discrepancy is small, more weight is assigned to the cue that is more reliable, i.e., leading to a smaller response variance, whereas when the discrepancy is large, more weight is assigned to the cue that is less ambiguous, such as path integration or the configuration of landmarks.

Plenty of studies have investigated the competition for cue weights between landmark and path integration in a conflict paradigm. In this paradigm, participants learn a target location with respect to landmarks and path integration. Then during test, the landmarks are moved so that the two cues indicate conflicting target locations. Previous studies show that if the discrepancy between the cues was small, human and non-human animal navigators assigned more weight to the landmark, which was the more reliable cue; whereas if the discrepancy was large, they relied on the path integration and ignored the landmark (Etienne, Teroni, Portenier, & Hurni, 1990; Foo et al., 2005; Shettleworth & Sutton, 2005; Zhao & Warren, 2015a). The path integration system was used as a reference system to detect whether the landmarks were stable or not (Cheng et al., 2007). When the discrepancy

between the path integration and the landmarks was large, the landmarks were considered as unstable. Zhao and Warren (2015b) manipulated the stability of landmarks in a navigational task. They found that, if landmarks were stable across learning and testing phases, participants assigned more weight to the landmarks, whereas if the landmarks were moved across learning and testing phase within each trial, participants assigned more weight to path integration. These studies suggested that cue weights are determined by cue reliability and cue stability. However, Chen and colleagues (2017) found that cue stability affected cue weights by modulating cue reliability. When landmarks were stable across trials, participants assigned more weight to the landmarks. However, when the landmarks were moved across trials, response reliability with respect to the landmarks decreased, which in turn reduced the weight assigned to the landmarks.

Cue competition between features and geometry in reorientation has also been investigated by moving the two cues relatively at test and forcing participants to choose among the geometrically correct corners, the featurally correct corner, and the incorrect corner (Figure 1.1). Studies have shown that the relative use of features and geometry when the two cues were in conflict was modulated by enclosure size. Ratliff and Newcombe (2008) investigated reorientation of human adults when the shape of a rectangular room and a distinctive fabric indicated conflicting responses. They found that participants were more likely to reorient with respect to the featural cue, which was the distinctive fabric, in a large room than in a small room. Studies on chicks and fish found that if a non-geometric feature, i.e., the color of a wall, was shifted with respect to the geometric shape of a rectangular room, the probability of choosing the geometrically correct corner decreased and the probability of

choosing the featurally correct corner increased as the room size increased (Sovrano & Vallortigara, 2006; Sovrano, Bisazzaa, & Vallortigara, 2007). However, these studies could not exclude the effect of overshadowing. The results that features were more likely to be used in a large room may be because features were less likely to be overshadowed by geometry in in a large room, or because features were given more weight in a large room. Therefore, it could not be concluded if the different relative use of the cues was due to the competition for cognitive resources during encoding or the competition for cue weights during retrieval, or both.



Figure 1.1. Illustration of the conflict paradigm in reorientation studies. Participants learn a target at one corner (denoted by X) with respect to the room geometry and a feature (e.g. a blue wall). At test, the feature is displaced relative to the room. The participants are forced to choose among the geometrically correct corners, the featurally correct corner and the incorrect corner.

Studies also suggest cue weights of features and geometry are modulated by cue stability. Chicks learned the location of food with respect to four patterned panels in a rectangular room. During the test, the size of the room was changed, and the panels were shifted with respect to the relative metric configuration of the walls. The probability of choosing the corner indicated by patterned panels was higher than the probability of choosing the corners indicated by the relative length of the walls (Chiandetti, Regolin, Sovrano, & Vallortigara, 2007). Ratliff and Newcombe (2008) found if room size remained consistent across learning and testing, human adults assigned more weight to the geometric cue in a small room, and assigned comparable weights to the geometric cue and the featural cue in a large room. However, if room size changed across learning and testing, human adults assigned more weights to the featural cue in both small and large rooms.

## 1.3 Factors that affect cue interaction in reorientation

Studies on cue interaction during reorientation have shown diverse results. Some studies suggest geometry has a predominant role during both the encoding and the retrieval phases of spatial memory, whereas other studies suggest the roles of geometry and features are interchangeable as the external environments and the internal states of navigators vary. In this section, I will discuss how cue interaction between geometry and features during reorientation is affected by two factors. Firstly, it is evident in previous studies that room size, as an environmental factor, modulates the interaction between geometry and features during both encoding and retrieval. Secondly, many studies have shown that navigators' long-term and short-term experiences also affect the interaction between geometry and features.

## **1.3.1** The effect of room size

The effect of room size has been widely found in reorientation of human adults, children and non-human animals. Despite that different materials and species were studied in those experiments, they all show the same trend that the role of geometry is weakened, and the role of features is strengthened as the environmental size increases. This phenomenon was found during both the encoding and the retrieval phases of reorientation.

Chiandetti and colleagues (2007) found that room size affected the competition between geometry and features during encoding. They had chicks learn the location of food with respect to four distinctive patterned panels in a rectangular room. At test, if the panels were removed, chicks were more likely to correctly use the geometric cue in a small room than in a large room. If the rectangular room was shifted to a square room, chicks were more likely to correctly use the featural cue in a large room than in a small room. These results suggest that geometry is more likely to be overshadowed by features as room size increases, whereas features are more likely to be overshadowed by geometry as room size decreases.

Studies on human adults, chicks and fish found that room size also affects the competition between geometry and features during retrieval (Ratliff & Newcombe, 2008; Sovrano & Vallortigara, 2006; Sovrano, Bisazzaa, & Vallortigara, 2007; Vallortigara, Feruglio, & Sovrano, 2005). Those studies found when room shape and wall features (a distinctive fabric or the color of a wall) conflicted, the probability of choosing the geometrically correct corner was higher in a small room than in a large room and the probability of choosing the featurally correct corner was higher in a large room than in a small room. Those results suggest navigators assign more weight to featural cues and less

weight to geometric cues as room size increases.

Other studies also show a similar trend that the relative use of features comparing to geometry increases as enclosure size increases. Learmonth, Nadel, and Newcombe (2002) found young children were able to use featural cues to reorient in a large room but not in a small room; Sovrano, Bisazzaa, and Vallortigara (2005) found fish made more errors using geometric cues when transferred from small to large space, and made more errors using featural cues when transferred from large to small space; Maes, Fontanari, and Regolin (2009) found rats were more likely to be attracted by featural cues and thus less used geometric cues in a larger room. However, those studies did not differentiate different phases of spatial reorientation. Therefore, cue interaction during encoding and retrieval confound with each other making the results hard to interpret.

Cue salience may be one component of the room size effect. Gouteux and colleagues (2001) kept the room size constant and changed the size of the featural cues. They found that monkeys were more likely to use featural cues when they are larger, i.e., more salient. In some cases, it is apparent that features are more salient in larger enclosures because features used in larger enclosures are larger than those used in small enclosures. For example, if the featural cue is a colored wall, as the room becomes larger, the colored wall also becomes larger. Sovrano and Vallortigara (2006) explained that besides the positive relationship between room size and the salience of featural cues, a negative relation between room size and the salience of a corner, navigators can see a larger portion of the room in a small room than in a large room, allowing them to infer the geometric relations among

different parts more easily in a smaller room (Figure 1.2). Miller (2009) tested the relation between the room size effect and cue salience by manipulating the salience of featural and geometric cues and simulating probability of choosing each corner during reorientation in an associative model (Miller & Shettleworth, 2008). He assumed the salience of a featural cue is greater in a large enclosure whereas the salience of a geometric cue is greater in a small enclosure, and successfully simulated the room size effect found in previous studies (Chiandetti et al., 2007; Learmonth et al., 2002; Sovrano & Vallortigara, 2006; Vallortigara et al., 2005). However, the model itself could not explain why cue salience of features should increase with room size and the successful simulation does not indicate a causal relationship between cue salience and room size.

Sovrano and colleagues (2005) speculated that features are more useful in larger rooms because navigators only use features beyond a certain distance as an orientational cue. This hypothesis was supported by neuroscience studies that head direction cells mostly followed distal landmarks when distal and proximal landmarks were in conflict (Yoganarasimha, Yu, & Knierim, 2006). It may be because when a navigator is close to a landmark, the relative orientation between them changes rapidly as the navigator moves and therefore is useful to identify the navigator's location, whereas if the navigator is far from the landmark, the orientation of the landmark almost remains stable and therefore can be used to identify an allocentric direction (Nadel & Hupbach, 2006; see also Stürzl & Zeil, 2007; Zeil et al., 2003).





Figure 1.2. Illustration of salience of room geometry in small and large rooms. Sovrano and Vallortigara (2006) proposed that geometric information, such as the lengths of the walls, is more easily observed in a smaller enclosure. When at a certain distance from a corner, a navigator could see a larger proportion of the room in a small room than in a large room.

# **1.3.2** The effect of experience

Other than the property of the environment, experience of navigators also contributes to cue interaction. Studies on non-human animals show that interaction between geometry and features is affected by long-term experience. Gray and colleagues (2005) argued that geometry was not found to be overshadowed by features in previous studies because the

animals tested in those experiments were reared in laboratories, thus were used to rightangled geometries. They tested reorientation of wild-caught mountain chickadees (Poecile gambeli) and found encoding of geometry was overshadowed by the presence of a feature adjacent to the target. When the geometric cue and the featural cue were in conflict, more weight was assigned to the featural cue adjacent to the target. Brown, Spetch, and Hurd (2007) found rearing environment modulates cue interaction between features and geometry during both encoding and retrieval phase of reorientation of fish. When only the geometric cue was available at test, although both fish raised in circular and rectangular tanks could reorient themselves, fish raised in the rectangular tank chose the geometrically correct corners more often than fish raised in a circular environment. Moreover, when both featural and geometric cues were presented and in conflict at test, fish raised in the circular tank assigned more weight to the featural cues than those raised in the rectangular tank. Twyman, Newcombe, and Gould (2013) found similar results on mice. However, the effect of longterm experience on interaction between features and geometry varies across species. Chiandetti and Vallortigara (2008, 2010) found chicks reared in both circular and rectangular environments spontaneously learned geometric cues indicating that the encoding of geometric cues was not overshadowed by featural cues. They also found that, when the featural cues and the geometric cues were in conflict, the relative use of the cues were not modulated by rearing environments.

The interaction between geometry and features is also affected by short-term experience. Twyman, Friedman, and Spetch (2007) found 4- and 5-years old children could be trained to reorient using featural cues. In their experiment, half of the children were pretrained in an equilateral triangle-shaped room and were then tested in a rectangular room with a yellow wall. Pretrained children were able to find the correct corner as indicated by the colored wall whereas children without pretraining equally searched between the two geometrically equivalent corners at the first four trials. Moreover, after four trials, those children without pretraining also learned to use the featural cue to find the correct corner.

Short-term experience also affects the weights of features and geometry during retrieval. Chiandetti and colleagues (2007) found chicks assigned more weight to featural cues than geometric cues if room size changed across learning and testing phases. Ratliff and Newcombe (2008) found similar results with human adults. They claimed that the experience of learning the featural cues in a large room where they were more salient encouraged participants to use the featural cues even in a small room where they were less salient than the geometric cues. Nevertheless, these results can also be interpreted that the competition between features and geometry is affected by experienced cue stability. Features, such as a panel, a tree, or the color of a wall, are less stable because they are moveable or changeable, whereas geometry, such as the shape of a room or the contour of a mountain, cannot be easily changed (Gallistel, 1990). Therefore, when the two cues are in conflict, normally people will think the featural cue has been moved. However, in the two studies mentioned above, the size of the room was changed across learning and testing phases, which made the navigators experienced an instability of the geometric cue and thus reduced the weight assigned to it.

## 1.4 Theories of cue interaction in reorientation

During decades of research in reorientation, scientists in this area have formed two camps and their theories can be categorized into two groups. One group of theories are called modularity theories, which support that geometry and features are two types of cues that have different processing mechanisms. The name comes from the very first theory in the area, the geometric module theory, which proposed that geometry is processed by a specific module. The other group of theories are call unified theories, which support that geometry and features share the same processing mechanism. In this section, I will discuss about the two groups of theories and their interpretations of cue interaction between geometry and features during reorientation.

## **1.4.1** The modularity theories

Based on the finding that rats could only use geometries but not features to reorient, Cheng (1986) proposed a geometric module theory suggesting there is a module called metric frame that only encodes the geometric information of surfaces. A module, according to its definition, must fulfill many properties such as domain specificity, encapsulation, and mandatory processing (Fodor, 1983). The strict definition limited the flexibility of the geometric module theory in explaining diverse findings in the area. Therefore, Lee and Spelke (2010a, b) proposed a two-system theory based on the original geometric module theory. They suggested that there are two independent systems: the geometric system processes extended surfaces in the environment, and it uses the distances and directions of surfaces to specify the position of the navigator; the featural system processes objects and 2D patterns in the environment, and it uses their distinctive properties to specify the location of the goals.

The common characteristic of those theories is that they both claim that the processing mechanisms of geometry and features are fundamentally different. This hypothesis is

supported by neuroscience studies showing that processing of boundary and isolated objects have different neural mechanisms. In a functional neuroimaging study, Doeller and colleagues (2008) found extended surfaces and isolated objects activated different brain areas. The right posterior hippocampus was found to be responsible for processing boundaries and the right dorsal striatum to be responsible for processing landmarks. Lever and colleagues (2009) discovered boundary vector cells in rats that only fire at a certain distance from a boundary but do not respond to isolated objects.

Independent processing of geometry and features is also supported by behavioral studies. Studies on fish, rats and human adults show that learning geometry overshadows learning features but not vice versa (Doeller & Burgess 2008; Hayward et al., 2003, 2004; Sovrano, Bisazza, & Vallortigara, 2003; Wall, Botly, Black, & Shettleworth, 2004). Moreover, feature-learning can be interfered with by many types of tasks which do not affect learning geometry. Cheng (1986) found that rats could use featural cues when the location of the target was fixed from trial to trial, but not when the location of the target was shifted from trial to trial, whereas rats could use geometric cues in both cases. Hermer-Vazquez and colleagues (1999) found human adults could use geometric cues but not featural cues to reorient while performing a verbal shadowing task. Ratliff and Newcombe (2008b) found performing a spatial visualization task impaired learning featural cues but did not interfere learning geometric cues. In sum, these findings suggest learning geometry is incidental because it is not subject to overshadowing effect; learning features, on the other hand, is suggested to be associative learning because it can be interfered by learning geometry and many other tasks.

The modularity theories are also supported by developmental studies showing that abilities of processing geometry and features mature at different age. Children as young as 18-24 months old can already use geometry to reorient, but they cannot use features to reorient until 5 years old (Hermer & Spelke, 1994, 1996; Hermer-Vazquez, Moffet & Munkholm, 2001). Based on the findings that the ability to use features to reorient correlated with language production ability, and that learning features, but not geometry, was overshadowed by a verbal task, researchers proposed that use of geometry is spontaneous, and use of features is partially dependent on human language (Hermer-Vazques et al., 1999). This idea is consistent with findings that some non-human animals can only use geometries but not features to reorient (Cheng, 1986). Moreover, use of geometry seems to be innate. Animals reared in both circular and rectangular environment could use geometric cues to reorient (Brown et al., 2007; Twyman et al., 2013). And most strikingly, chicks hatched in the darkness who had completely no experience of navigation through geometry could reorient with respect to the shape of the testing room when they were exposed to it for the first time (Chiandetti, Spelke, & Vallortigara, 2015).

Although the modularity theories demonstrated an interesting way to explain the differences between learning features and geometry and inspired many researchers, they have long been doubted because of a lack of flexibility. The modularity theories cannot explain that featural cues are preferred by some non-human animals that cannot use language (Sovrano, Bisazza, & Vallortigara, 2005, 2007), that the relative use of features and geometry can be affected by various factors such as room size and navigators' experience (Brown et al., 2007; Chiandetti et al., 2007; Learmonth et al., 2002; Ratliff & Newcombe, 2008; Sovrano &

Vallortigara, 2006; Sovrano, Bisazzaa, & Vallortigara, 2007; Twyman et al., 2013), and especially that learning of geometry can be overshadowed by learning of features in certain circumstances (Gray, Bloomfield, Ferrey, Spetch, & Sturdy, 2005; Pearce, Graham, Good, Jones, & McGregor, 2006).

#### **1.4.2** The unified theories

In contrast to the modularity theories, some researchers believe learning features and geometry share similar mechanisms. In the view matching theory (Stürzl & Zeil, 2007; Zeil et al., 2003), geometry and features in the environment are broken down into pixels. Navigators can reach a destination just by matching their current view with the snapshot they took at the goal without recognizing any boundaries or landmarks. In the associative theory (Miller & Shettleworth, 2007, 2008; Miller, 2009), navigators learn geometry and features by gaining associative strength between the reward and each specific cue when they search at a certain location. In the adaptive combination theory (Newcombe & Huttenlocher, 2006; Newcombe & Ratliff, 2007), features and geometry are simply two kinds of cues that can be combined in a Bayesian fashion. The weight of each cue depends on the properties of that cue, such as its certainty, salience, and validity.

The common characteristic of the theories mentioned above is that they all suggest that geometry and features are not fundamentally different from each other. They claim the underlying processing mechanisms of features and geometry are similar and the interaction between geometry and features varies as their properties vary in different environments. The main advantage of this group of theories is flexibility. They could explain the diversity of findings regarding overshadowing and blocking effects during encoding and relative use of
geometry and features during retrieval of reorientation (for review, see Cheng & Newcombe, 2005). The room size effect is a strong evidence supporting the unified theories. Researchers claim that the interaction between features and geometry is different in a small room or in a large room because their relative salience changed as the room size changed. This hypothesis is supported by a simulation using an associative model (Miller, 2009) and the finding that the reliability of featural cue increases as the enclosure size increases (Sovrano, Bisazzaa, & Vallortigara, 2005).

Another piece of evidence for similar mechanisms for learning of features and geometry is the facilitation effect. Some studies found that feature learning and geometry learning sometimes facilitated each other (Graham et al., 2006; Pearce, Ward-Robinson, Good, Fussell, & Aydin, 2001; Sturz, Brown, & Kelly, 2009; Sturz, Kelly, &Brown, 2010). The facilitation effect between features and geometry can be explained by both the associative theory (Miller & Shettleworth, 2007, 2008) and super-additive integration (Mou & Spetch, 2013). The associative theory suggested geometry and features compete for associative strength when the navigator finds a reward in the correct corner. Learning a featural cue can increase the probability of successful searching and thus increases the associative strength between the reward and the geometric cue. The facilitation effect also suggests the features and geometry may be integrated in a super-additive way. Mou and Spetch (2013) found that the performance of change detection using multiple cues can be better than the sum of performance using each single cue. They suggested that in addition to integrating the cues in a Bayesian way, people also form an additional representation of the overall configuration of the cues. It is also suggested that the representations of each single cue are not independent of each other if they can be integrated into an additional representation.

The unified theories also have limitations. The view matching theory (Stürzl & Zeil, 2007; Zeil et al., 2003), which hypothesizes reorientation does not involve any high-level processing, is only applicable to insects, but not highly evolved animals, such as mammals. The associative theory (Miller & Shettleworth, 2007, 2008; Miller, 2009) is flexible in explaining diverse results because it assumes the learning rates of geometry and features vary in different environments. However, there is no independent criterion to determine the learning rates. Similar issue troubles the adaptive combination theory (Newcombe & Huttenlocher, 2006; Newcombe & Ratliff, 2007) which hypothesizes that competition between features and geometry is determined by properties of the cues such as salience, stability and validity. However, without clear definitions of those properties, this theory cannot be rigorously evaluated.

Another challenge to the unified theories is to explain the dominant role of geometry found in numerous studies. The adaptive combination theory suggests that geometry was dominant in most of the previous studies simply because it was more salient in those environmental settings (Newcombe & Huttenlocher, 2006). However, it is still unclear what salience is and why geometry is more salient than features. Huttenlocher and Lourenco (2007) demonstrated that this may be because geometry is a relative cue which vary along one dimension (short vs long), whereas a feature is a non-relative cue (red vs blue), and relative cues are easier to use than non-relative cues. In a typical reorientation paradigm in which young children were found to only use the geometric cues but not the featural cues, the geometric cues were relative lengths or distances and the featural cues were non-relative colors or patterns. Huttenlocher and Lourenco (2007) had children tested in square rooms with relative features (small and large dots) or non-relative features (blue and red walls) and found that only those who were tested with relative features performed above chance level. Experiments with mice also confirmed that using a categorical cue is more difficult than using a continuous cue (Twyman, Newcombe, & Gould, 2009). However, this theory cannot explain why angles, which are relative cues, function like features rather than geometry (Kelly et al., 2011; Sturz et al., 2011; Sturz et al., 2012).

In a multiple-reference-point theory, Mou and Zhou (2013) suggested that the advantage of a geometric cue over a featural cue is that a geometric cue as an extended surface has an infinite number of reference points while a featural cue as a single landmark only has one reference point. They suggested more boundary vector cells may be activated when more reference points are available. In addition, multiple reference points that form a regular shape make it easier to establish a frame of reference. In an earlier study, Doeller and Burgess (2008) found, during goal localization, a boundary overshadowed a single landmark but not vice versa. In the study of Mou and Zhou (2013), a circular array of 36 identical landmarks was used instead of a single landmark and no overshadowing effect was observed. The result shows that features are equivalent to geometries if they provide enough reference points. However, this study was done in a goal localization paradigm. Whether the conclusion can be extended to reorientation needs further tests.

# 1.5 Goal of current work

So far, I have reviewed most of the important studies and theories in reorientation area. We can see that the findings regarding the interaction between geometry and features are

quite diverse which lead to a long-lasting debate between the modularity theories and the unified theories. Both groups of theories have their strengths and limitations. On one hand, the modularity theories brought up an interesting way to understand how different cues are processed during spatial reorientation, but they lack flexibility to explain the diversity of interaction between features and geometry. On the other hand, the unified theories are quite flexible but some of their components lack strict definitions which weakened their power of explanation. The room size effect, for example, seems to support the unified theories because the modularity theories would predict geometry to be dominant in both small and large rooms. The unified theories explain that the salience of the cues changed with room size. However, it is not clear why the salience of geometry or feature should change with room size because those theories neither have a clear definition of salience nor a method to measure salience. Therefore, we cannot conclude whether the increased use of features in a larger room is due to increase salience of features, decreased salience of geometry or other factors.

In this dissertation, my colleagues and I will dissociate and examine cue competition during encoding, combination during retrieval and competition during retrieval in a reorientation paradigm. Competition during encoding is examined by comparing the performance of using a single cue after learning that cue with the performance of using that single cue after learning that cue and an additional cue. Combination during retrieval is examined by comparing the performance of using both cues with the sum of performances of using each single cue. Competition during retrieval is examined by comparing the performance of both cues when they are in conflict with the performance estimated by the

relative response accuracy of using each cue. The purpose of this dissertation is to use these methods to investigate how various factors modulate cue interaction between features and geometry during reorientation.

Specifically, the first goal of this dissertation is to investigate the effect of familiarity on the interaction between features and geometry during reorientation. Familiarity is an important factor that has been overlooked. As suggested by previous studies, use of features and geometry can be affected by the navigators' short-term experiences (Chiandetti et al., 2007; Ratliff & Newcombe, 2008; Twyman, Friedman, & Spetch, 2007). Thus, it is reasonable to speculate that navigators modify their strategies as they gain more experience in an environment. In other words, familiarity with an environment may affect cue interaction in reorientation. The second goal of this dissertation is to investigate the effect of room size on the relative use of features and geometry during reorientation. As mentioned in the introduction, room size effect has been demonstrated in many studies. However, its underlying mechanism has not been fully understood. This dissertation aims to provide an explanation of the room size effect in reorientation.

Two studies investigated how various cues interact during reorientation of human adults. Study 1 tested the interaction between buildings and street configurations in outdoor environments. We examined the effect of familiarity on competition during encoding, combination during retrieval and competition during retrieval. Study 2 tested the interaction between room geometry and features in indoor environments. We examined the effects of familiarity and room size on combination and competition during retrieval.

#### 1.6 **References**

- Bayes, T. (1763). An essay towards solving a problem in the doctrine of chances. *Philosophical Transactions*, *53*, 370-418.
- 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.
- Brown, A. A., Spetch, M. L., & Hurd, P. L. (2007). Growing in circles rearing environment alters spatial navigation in fish. *Psychological Science*, *18*(7), 569-573.
- Buckley, M. G., Smith, A. D., & Haselgrove, M. (2016). Thinking outside of the box:
  Transfer of shape-based reorientation across the boundary of an arena. *Cognitive Psychology*, 87, 53–87.
- Chen, X., McNamara, T. P., Kelly, J. W., & Wolbers, T. (2017). Cue combination in human spatial navigation. *Cognitive Psychology*, *95*, 105–144.
- Cheng, K. (1986). A purely geometric module in the rat's spatial representation. *Cognition,* 23(2), 149-178.
- Cheng, K. (2008). Whither geometry? Troubles of the geometric module. *Trends in Cognitive Sciences*, *12*, 355–361.
- Cheng, K., & Newcombe, N. S. (2005). Is there a geometric module for spatial orientation? Squaring theory and evidence. *Psychonomic Bulletin & Review*, *12*, 1–23.
- Cheng, K., Shettleworth, S. J., Huttenlocher, J., & Rieser, J. J. (2007). Bayesian integration of spatial information. *Psychological Bulletin*, *133*(4), 625–637.

- Chiandetti, C., Regolin, L., Sovrano, V., & Vallortigara, G. (2007). Spatial reorientation: The effects of space size on the encoding of landmark and geometry information. *Animal Cognition*, *10*, 159–168.
- Chiandetti, C., Spelke, E. S., & Vallortigara, G. (2015). Inexperienced newborn chicks use geometry to spontaneously reorient to an artificial social partner. *Developmental Science*, *18*(6), 972–978.
- Chiandetti, C., & Vallortigara, G. (2008). Is there an innate geometric module? Effects of experience with angular geometric cues on spatial re-orientation based on the shape of the environment. *Animal Cognition*, *11*(1), 139–146.
- Chiandetti, C., & Vallortigara, G. (2010). Experience and geometry: Controlled-rearing studies with chicks. *Animal Cognition*, *13*(3), 463–470.
- 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*, 105(15), 5915-5920.
- Du, Y., Mahdi, N., Paul, B., & Spetch, M. L. (2016). Cue salience influences the use of height cues in reorientation in pigeons (Columba livia). *Journal of Experimental Psychology: Animal Learning and Cognition*, 42(3), 273–280.
- Du, Y., Spetch, M. L., & Mou, W. (2016). Look up: Human adults use vertical height cues in reorientation. *Memory & Cognition*, 44, 1277-1287.

Fodor, J. A. (1983). The modularity of mind: An essay on faculty psychology. MIT press.

Foo, P., Warren, W. H., Duchon, A., & Tarr, M. J. (2005). Do humans integrate routes into a cognitive map? Map- versus landmark-based navigation of novel shortcuts. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 31(2), 195–215.

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

- 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.
- Gouteux, S., Vauclair, J., & Thinus-Blanc, C. (2001). Reorientation in a small-scale
  environment by 3-, 4-, and 5-year-old children. *Cognitive Development*, 16(3), 853-869.
- Gouteux, S., & Spelke, E. S. (2001). Children's use of geometry and landmarks to reorient in an open space. *Cognition*, *81*(2), 119-148.
- 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*, 44–59.
- Gray, E. R., Bloomfield, L. L., Ferrey, A., Spetch, M. L., & Sturdy, C. B. (2005). Spatial encoding in mountain chickadees: Features overshadow geometry. *Biology Letters*, 1, 314–317.
- 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*, 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. *The Quarterly Journal of Experimental Psychology: Section B*, 56(1), 114-126.
- Hermer, L., & Spelke, E. S. (1994). A geometric process for spatial reorientation in young children. *Nature*, *370*, 57–59.
- Hermer, L., & Spelke, E. (1996). Modularity and development: The case of spatial reorientation. *Cognition*, *61*, 195–232.
- 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., & Kastsnelson, A. S. (1999). Sources of flexibility in human cognition: Dual-task studies of space and language. *Cognitive Psychology*, 39(1), 3-36.
- Hu, Q., Zhang, J., Wu, D., & Shao, Y. (2015). Is height a core geometric cue for navigation?
  Young children's use of height in reorientation. *Journal of Experimental Child Psychology*, 130, 123–131.
- Hupbach, A., & Nadel, L. (2005). Reorientation in a rhombic environment: No evidence for an encapsulated geometric module. *Cognitive Development, 20*(2), 279-302.
- Huttenlocher, J., & Lourenco, S. F. (2007). Coding location in enclosed spaces: Is geometry the principle? Developmental Science, 10(6), 741–746.

- Kamin, L. J. (1969). Predictability, surprise, attention and conditioning. In B. A. Campbell &
  R. M. Church (Eds.), *Punishment and aversive behavior*, (pp. 276–296). New York: Appleton-Century-Crofts.
- Kelly, D. M., Chiandetti, C., & Vallortigara, G. (2011). Re-orienting in space: Do animals use global or local geometry strategies? *Biology Letters*, 7,372–375.
- 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., Sheridan, N., & Jones, M. (2008). Why size counts: Children's spatial reorientation in large and small enclosures. *Developmental Science*, 11, 414–426.
- Lee, S. A., & Spelke, E. S. (2010a). Two systems of spatial representation underlying navigation. *Experimental Brain Research*, 206(2), 179-188.
- Lee, S. A., & Spelke, E. S. (2010b). A modular geometric mechanism for reorientation in children. *Cognitive Psychology*, *61*(2), 152-176.
- Lee, S. A., & Spelke, E. S. (2011). Young children reorient by computing layout geometry, not by matching images of the environment. *Psychonomic Bulletin & Review*, 18(1), 192–198.
- 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, 144-161.

- Lever, C., Burton, S., Jeewajee, A., O'Keefe, J., & Burgess, N. (2009). Boundary vector cells in the subiculum of the hippocampal formation. *Journal of Neuroscience*, 29, 9771– 9777.
- Lubyk, D. M., Dupuis, B., Gutiérrez, L., & Spetch, M. L. (2012). Geometric orientation by humans: angles weigh in. *Psychonomic Bulletin & Review, 19*(3), 436-442.
- Maes, J. H., Fontanari, L., & Regolin, L. (2009). Spatial reorientation in rats (Rattus norvegicus): use of geometric and featural information as a function of arena size and feature location. *Behavioural Brain Research*, 201(2), 285-291.
- Miller, N. Y. (2009). Modeling the effects of enclosure size on geometry learning. Behavioural Processes, 80, 306–313.
- Miller, N. Y., & Shettleworth, S. J. (2007). An associative model of geometry learning. Journal of Experimental Psychology: Animal Behavior Processes, 33, 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*, 419–422.
- Mou, W., & Spetch, M.L. (2013) Object location memory: Integration and competition between multiple context objects but not between observers' body and context objects. *Cognition*, 126(2), 181-197.
- Mou, W., & Zhou, R. (2013). Defining a boundary in goal localization: Infinite number of points or extended surfaces. *Journal of Experimental Psychology: Learning, Memory,* and Cognition, 39(4), 1115.

- Nadel, L., & Hupbach, A. (2006). Cross-species comparisons in development: the case of the spatial 'module'. *Attention and performance XXI*, 499-511.
- 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.
- 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., & Huttenlocher, J. (2006). Development of spatial cognition. In D. Kuhn & R. S. Siegler (Eds.), *Handbook of child psychology: Cognition, perception, and language*, vol. 2 (6th ed., pp. 734–776). New York: Wiley.
- Newcombe, N. S., & Ratliff, K. R. (2007). Explaining the development of spatial reorientation: Modularity-plus-language versus the emergence of adaptive combination. In J. M. Plumert & J. P. Spencer (Eds.), *The emerging spatial mind*, (pp. 63–76). New York: Oxford University Press.
- 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.

Pavlov, I. P. (1927). Conditioned reflexes. New York: Dover.

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.

- Pearce, J. M., Ward-Robinson, J., Good, M., Fussell, C., & Aydin, A. (2001). Influence of a beacon on the spatial learning based on the shape of the test environment. *Journal of Experimental Psychology: Animal Behavior Processes*, 27, 329–344.
- 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.
- 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,* 199–210.
- Sovrano, V. A., Bisazza, A., & Vallortigara, G. (2005). Animals' use of landmarks and metric information to reorient: Effects of the size of the experimental space. *Cognition*, 97, 121–133.
- Sovrano, V. A., Bisazza, A., & Vallortigara, G. (2007). How fish do geometry in large and in small spaces. *Animal Cognition*, *10*, 47–54.
- Sovrano, V. A., & Vallortigara, G. (2006). Dissecting the geometric module: A sense linkage for metric and landmark information in animals' spatial reorientation. *Psychological Science*, *17*(7), 616-621.

- Sturz, B. R., Brown, M. F., & Kelly, D. M. (2009). Facilitation learning spatial relations among locations by visual cues: Implications for theoretical accounts of spatial learning. *Psychonomic Bulletin & Review*, 16, 306–312.
- 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 & 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, 246–253.
- Sturz, B. R., Kelly, D. M., & Brown, M. F. (2010). Facilitation of learning spatial relations among locations by visual cues: Generality across spatial configurations. *Animal Cognition*, 13, 341–349.
- Stürzl, W., & Zeil, J. (2007). Depth, contrast and view-based homing in outdoor scenes. Biological Cybernetics, 96, 519–531.
- 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.
- Twyman, A. D., Newcombe, N. S., & Gould, T. J. (2009). Of mice (Mus musculus) and toddlers (Homo sapiens): Evidence for species-general spatial reorientation. *Journal* of Comparative Psychology, 123(3), 342–345.

- Twyman, A. D., Newcombe, N. S., & Gould, T. J. (2013). Malleability in the development of spatial reorientation. *Developmental Psychobiology*, *55*(3), 243–255.
- Vallortigara, G. (2009). Animals as natural geometers. In L. Tommasi, M. A. Peterson, & L. Nadel (Eds.), *Cognitive biology* (pp. 83–104). Cambridge: MIT Press.
- Vallortigara, G., Feruglio, M., & Sovrano, V. A. (2005). Reorientation by geometric and landmark information in environments of different sizes. *Developmental Science*, 8, 393–401.
- 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. *Learning & Behavior*, 32, 289– 298.
- Waller, D., & Lippa, Y. (2007). Landmarks as beacons and associative cues: Their role in route learning. *Memory & Cognition*, 35(5), 910–924.
- Wang, L., Mou, W., & Sun, X. (2014). Development of landmark knowledge at decision points. *Spatial Cognition & Computation*, 14(1), 1-17.
- 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*, 1369–1376.
- Yoganarasimha, D., Yu, X., & Knierim, J. J. (2006). Head direction cell representations maintain internal coherence during conflicting proximal and distal cue rotations:
   Comparison with hippocampal place cells. *Journal of Neuroscience*, *26*(2), 622–631.
- Zeil, J., Hofmann, M. I., & Chahl, J. S. (2003). Catchment areas of panoramic snapshots in outdoor scenes. *Journal of the Optical Society of America*, 20, 450–469.

Zhao, M., & Warren, W. H. (2015). Environmental stability modulates the role of path integration in human navigation. *Cognition*, *142*, 96–109.

# Chapter 2 Cue Interaction between Buildings and Street Configurations during Reorientation in Familiar and Unfamiliar Outdoor Environments

A version of this work was previously published as: Wang, L., Mou, W., & Dixon, P. (2018). Cue interaction between buildings and street configurations during reorientation in familiar and unfamiliar outdoor environments. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 44*(4), 631-644.

#### 2.1 Abstract

Two experiments investigated the effect of familiarity on the interaction between buildings and street configurations during reorientation in large-scale outdoor environments. In immersive virtual environments, participants learned objects' locations in an intersection consisting of four streets. The objects' locations were specified by two cues: a building and/or the street configuration. During the test, participants localized objects with either or both cues. Participants were divided into a competition group and a no-competition group. The competition group learned both cues whereas the no-competition group learned the single cue for trials with single cue. For the trials with both testing cues, both groups learned both cues and these two cues were placed at the original locations or displaced relative to each other during testing. Critically, the familiarity with the environment was also manipulated: in Experiment 1, participants learned the same building at the same corner of the same intersection for all trials (familiar); in Experiment 2, participants learned different buildings at different corners of different intersections across trials (unfamiliar). The results showed that the performance in the competition group was impaired in unfamiliar environments but not in familiar environments. When displacement occurred, the participants' preference in unfamiliar environments was determined by the response accuracy of using the two cues respectively, whereas participants in the familiar environment preferred the street configuration with a probability higher than what was solely determined by response accuracy based on individual cues. When the two cues were consistent with each other, they were combined additively in both familiar and unfamiliar environments. The

results suggested that cue competition during encoding and retrieval is modulated by navigators' familiarity with the environment.

#### 2.2 Introduction

Reorientation is an important behavior for humans and non-human animals.

Reorienting in outdoor environments is especially critical for survival. During foraging and homing, wild animals must be able to regain their orientation using trees, rocks or the shape of a river when they are disoriented in a forest. Likewise, humans must be able to regain their orientation using signs, buildings or the configuration of streets when they are disoriented in a city. Although scientists have gained great understandings on reorientation in indoor environments since the study of Cheng (1986), investigation on outdoor reorientation of human adults is rare. The purpose of this study is to examine cue interaction in outdoor reorientation of human adults. Before we further specify the questions of the current study, we will first review the relevant studies examining cue interaction in indoor reorientation. We will then propose a general research procedure to study cue interaction. We will finally frame the questions of the current study by applying the general research procedure to reorientation in outdoor environments.

In a seminal study, Cheng (1986) trained rats to search for food hidden at one of the four corners in a rectangular room with four different panels in the corners. During the test, rats searched for the food after being disoriented. Instead of searching in the correct corner, the rats divided their search between the correct corner and the corner diagonally opposite to the correct corner, which is geometrically equivalent to the correct corner. This result indicated that rats only used the shape of the room to distinguish the geometrically correct corners but did not use the panels to avoid the corner diagonally opposite to the correct corner. Hermer and Spelke (1994, 1996) found that children between 18 and 24 months old

were able to use the shape of the room to search for a hidden toy. However, they could not use the featural cues such as the colors of the walls or distinctive objects to guide their search. Following these pioneer studies, an enormous number of studies examined the relative importance of geometry and features in reorientation (e.g. Brown, Spetch, & Hurd, 2007; Learmonth, Newcombe, & Huttenlocher, 2001; Lee & Spelke, 2010; Twyman, Friedman, & Spetch, 2007; for review, see Cheng, Huttenlocher, & Newcombe, 2013).

There are also studies that contrasted two cues other than geometry and features in reorientation. Recently, several studies contrasted different geometry cues in reorientation. For example, angles of corners in a room were contrasted with the shape of the room (e.g., Lubyk, Dupuis, Gutiérrez, & Spetch, 2012; Sturz, Forloines, & Bodily, 2012). The horizontal shape of a room were contrasted with vertical height cues in the room, including tilted floor (e.g., Nardi, Newcombe, & Shipley, 2011) and walls with different heights (Du, Spetch, & Mou, 2016). There are also studies that compared the boundary of an enclosed environment with a single landmark or a landmark array in reorientation (see Lew, 2011, for a review).

Regardless of the types of cues that were contrasted, most of the studies in reorientation examined cue competition either in encoding orientations or in regaining orientations after disorientation. In the former case, studies primarily investigated whether two different cues (e.g. geometrical and featural cues) compete for the encoding resources (e.g., Pearce, Graham, Good, Jones, & McGregor, 2006). In the latter case, studies primarily investigated whether people prefer one cue to the other cue when the two cues indicate different orientations (e.g., Ratliff & Newcombe, 2008). However, to our knowledge, studies that examined cue competition in both encoding and retrieving phases in one reorientation experiment are rare. We believe that in order to understand cue competition in reorientation more completely, we should examine cue competition in both encoding and retrieval phases in the same experiment.

Besides cue competition, cue combination is the other important type of cue interaction. In cue combination, people combine estimations indicated by two cues to improve their estimation. Cue combination has been examined in several spatial behaviors including homing (Chen & McNamara, 2014; Chen, McNamara, Kelly, & Wolbers, in press; Legge, Wystrach, Spetch, & Cheng, 2014; Nardini et al., 2008; Zhao & Warren, 2015a) and object localization (Holden, Newcombe, & Shipley, 2013; Huttenlocher, Hedges, & Duncans, 1991; Mou & Spetch, 2013; Sampaio & Wang, 2009). Cue combination is usually illustrated by variance reduction in spatial judgments when both cues are available than when either cue is available (Cheng et al., 2007). However, in a typical reorientation paradigm, reorientation performance is measured in terms of accuracy in choosing the correct location and judgment variance within a participant is usually not available. Therefore, cue combination is rarely examined in reorientation (Xu, Regier, & Newcombe, 2017).

In this study, we propose that to understand cue interaction in reorientation completely, we should examine both cue competition and cue combination in a single reorientation experiment (Mou & Spetch, 2013). In particular, a standard procedure to study cue interaction in reorientation should, in one single experiment, examine three types of cue interaction: cue competition in encoding orientations, cue combination in retrieving orientations when two cues indicate the same orientation, and cue competition in retrieving orientations when two cues indicate different orientations.

Moreover, to our knowledge, research on cue interaction during reorientation of human adults in an outdoor large-scale environment is rare. In the previous studies with human adults, participants were usually tested in room-size environments. As suggested in previous research, the size of the environment could change the strategies used by human adults in reorientation (Ratliff & Newcombe, 2008; Sturz & Kelly, 2013). Reorientation to broader outdoor environments (e.g., a city) is indeed a more common spatial task and more critical to survival (Mou et al., 2014). In everyday life, people can visually apprehend the local environment (e.g., a room) from a single viewpoint whereas they have to locomote considerably to apprehend an outdoor large-scale environment (Montello, 1993). Thus, it is much less likely that people lose their orientation in a local environment (i.e., a room) than in an outdoor large-scale environment. Therefore, it is more important to study how human adults reorient in outdoor large-scale environments.

In the current study, human adults regained their orientation in a city after disorientation. We examined two cues: a building in one corner of an intersection of four streets and the configuration of the streets (Figure 1). We acknowledge that there is no clear theoretical motivation to examine cue interaction between a building and a street layout. One may claim that the distinction between a building and a configuration of the streets is an example of the distinction between features and geometries. However, as a building has its own geometrical shape, we do not hold such claim. We chose buildings and street layouts primarily because they are two common cues in a city (Siegel & White, 1975). Following the standard procedure of studying cue competition proposed above, we investigated: (1) whether learning a building and learning a street configuration compete for common cognitive resources during encoding; (2) whether these two cues are additively combined in determining orientation after disorientation when these two cues indicate the same orientation; and (3) how these two cues are preferred after disorientation if they indicate two difference orientations.

We used the overshadowing paradigm to investigate whether learning a building and learning a street layout compete for common cognitive resources during encoding. The overshadowing paradigm is widely used to investigate the competition between two cues presented simultaneously during learning a response to a stimulus (Pavlov, 1927). Specifically, when Cue A overshadows Cue B, behaviorally the performance of localizing the target is better after individuals learn the target with the presence of only B than after individuals learn the target with the presence of both A and B.

Asymmetrical overshadowing effects, that is, Cue A overshadows Cue B but Cue B does not overshadow Cue A, are used to support Cue A is the dominant cue. For example, some studies showed that an enclosed shape overshadowed a landmark but not vice versa (Doeller & Burgess, 2008; Sovrano, Bisazza, & Vallortigara, 2003; Wall, Botly, Black, & Shettleworth, 2004). Therefore, the enclosed shape was the dominant cue. In contrast, symmetrical overshadowing effects, that is, Cue A and Cue B overshadow each other, are used to support that two cues are equally important. For example, other studies showed that landmarks could also overshadow an enclosed shape (Gray, Bloomfield, Ferrey, Spetch, & Sturdy, 2005; Pearce, Graham, Good, Jones, & McGregor, 2006; Wilson & Alexander, 2008). Therefore, an enclosed shape and a landmark are equally important in these studies. In the current study, asymmetrical overshadowing effects will be interpreted to mean that the

overshadowing cue is more dominant over the overshadowed cue; symmetrical overshadowing effects will be interpreted to mean that these two cues compete for the common cognitive resources and are equally important; finally no overshadowing effect will be interpreted to mean that these two cues do not compete for the common cognitive resources.

To test whether the cues of a building and a configuration of streets are additively combined in the retrieval phase of reorientation, we tested whether the cue leading to a more accurate response has a larger contribution to reorientation. Bayesian combination is one example of additive combination and has been examined in the field of spatial cognition (Chen & McNamara, 2014, Chen et al., in press; Cheng et al., 2007; Mou & Spetch, 2013; Nardini et al., 2008; Zhao & Warren, 2015a). Bayesian combination predicts that two cues are combined additively to reduce the inaccuracy (variance) of estimation; and that the weights of cues are inversely proportional to the relative inaccuracy (variance) using either cue individually. In a typical reorientation study, measurement of variance is not easy. Usually, the reorientation performance was measured in accuracy. In the current study, we proposed an accuracy-based combination model (see detailed specifications in General Method below) and tested whether the cue that leads to a higher response accuracy when being presented alone has a larger contribution to reorientation when both cues are available and indicate a consistent orientation during testing.

In addition, we also investigated how the cues of a building and a configuration of streets are preferred in the retrieval phase of reorientation when they indicate different orientations. In particular, we are interested in investigating whether people prefer a cue that

leads to a more accurate reorientation. Ratliff and Newcombe (2008) used a conflicting cue paradigm to examine cue preference in indoor reorientation. In their experiment, participants learned the location of a hidden target with respect to both featural and geometric cues in a large rectangular room or in a small rectangular room. Then, participants were tested with the featural cue being moved to one adjacent wall so that there was a conflict between the featural cue and the geometric cue. The results showed that participants in a large room were more likely to choose the corner indicated by the featural cue, while participants in a small room were more likely to choose the corner indicated by the geometric cue. The authors claimed that human adults gave more weight to the cue that was more salient, assuming the geometric cue is more salient in a small room and the featural cue is more salient in a large room. In the current study, we also used the conflicting cue paradigm. We tested whether the cue that leads to a higher response accuracy when being presented alone has a larger contribution to reorientation when both cues are available but indicate conflicting orientations during testing.

Most importantly, we hypothesized that the interactions, especially competition in encoding and combination in retrieval, between the building and the street configuration are modulated by the degree of participants' familiarity with the city. This hypothesis is based on the following speculations: the more familiar with an environment, the more likely people encode the spatial relations between buildings and street configurations; whether people encode the spatial relations between buildings and street configurations or not will modulate cue competition during encoding and retrieval of orientations.

A mental representation of the spatial relations between buildings and street configurations might reduce the cue competition in encoding orientations. There are at least two possible mechanisms for such reduction. First, people who have encoded the relations between the two cues may easily find the other cue when they see one cue. Such cue facilitation may counteract the cue competition for the common cognitive resource in encoding orientations relative to individual cues. Second, people may also encode the spatial relations between buildings and street configurations as well as their orientations relative to individual cues. Because encoding the spatial relations between buildings and street configurations consumes cognitive resources, fewer cognitive resources are left for encoding orientations in terms of each individual cue, producing cue competition. Therefore, cue competition is smaller for people who have already encoded the relations between buildings and street configurations<sup>1</sup>. Note that we do not distinguish between these two mechanisms empirically in the current study. As speculated above, as people become more familiar with an environment, they are more likely to encode the spatial relations between buildings and street configurations. Therefore, the effect of cue competition in encoding orientations is reduced or eliminated in a familiar environment but not in a novel environment.

A mental representation of the relations between buildings and street configurations might modulate cue preference during the retrieval phase when these two cues indicate different orientations. People who have not encoded the relations between two cues should not be able to detect the relative displacement between these two cues. Therefore, they may combine estimates based on each cue by giving more weight to the cue producing a more

<sup>&</sup>lt;sup>1</sup> We grateful to one anonymous reviewer for the suggestion of the second mechanism.

accurate response, assuming that people can know which cue results in a more accurate response similar to the assumption that people know which cue results in a more variable response in the cue combination literature (Chen & McNamara, 2014; Cheng et al., 2007; Mou & Spetch, 2013; Nardini et al., 2008; Zhao & Warren, 2015a). In contrast, people who have encoded the relations between two cues should be able to detect the relative displacement between the two cues. Therefore, cue preference may be affected not only by the response accuracy based on individual cues but also by other cognitive factors including participants' belief of the stability of cues. A cue resulting in a more accurate response might not be the cue that participants believe to be more stable, just as a cue resulting in less variable response might not be perceived to be more stable (Etienne & Jeffery, 2004; Foo et al., 2005; Zhao & Warren, 2015b). Therefore, in a novel environment, cue preference in the retrieval phase of reorientation is determined by response accuracy using individual cues whereas in a familiar environment, cue preference in the retrieval phase of reorientation may also be affected by people's belief of cue stability. Note that no prior theory can predict which cue, a building or a street configuration, is more stable.

In summary, the purpose of the current study was to examine cue interaction between a building and a street configuration in reorientations in a large-scale environment, more specifically, cue competition during encoding orientations, and cue combination and cue competition in retrieval of orientation. Furthermore, we investigated whether the cue competition between a building and a street configuration in reorientation, both during encoding and retrieval, are modulated by people's familiarity with the environment.

#### 2.3 General Method

Two experiments were conducted to examine cue interaction between a building and a street configuration. These two experiments were identical except that Experiment 1 used a familiar environment, whereas Experiment 2 used an unfamiliar environment. The method to manipulate the familiarity will be discussed in each experiment. Here, we describe the common materials, design, procedure, and the method of data analyses.

#### 2.3.1 Materials and Design

The experiments were conducted in a physical room that was 4 m by 4 m. A swivel chair was placed in the middle of the room. A virtual environment was displayed in stereo with an nVisor SX60 head-mounted display (HMD) (NVIS, Inc. Virginia). Each participant was placed in an InterSense IS-900 motion tracking system (InterSense, Inc., Massachusetts) so that participants could look around in the virtual environment. The virtual environment was a city consisting of four streets and a building as well as three identical trees (Figure 1). Each participant had 16 trials, each consisting of a learning phase and a testing phase. In the learning phase of each trial, participants learned the location of four objects (lock, candle, wood, and bottle, all fitting within approximate 50 cm) that were located at the end of each street respectively. In the testing phase of each trial, participants were required to locate two of the four objects. The locations of the objects differed across trials as in a working memory paradigm (Cheng, 1986).

Participants could rely on two kinds of cues to locate the objects: the building and the configuration of the streets (Figure 2.1). When there was a building cue, the building was located at one of the corners of the intersection. At the other three corners were three identical trees. When there was no building cue, the building was substituted by a tree identical to those at the other three corners. When there was a street configuration cue, the street configuration consisted of two short streets and two long streets. The streets were surrounded by walls that were 5 m tall. Like the building, the street configuration cues in the current research could also be used to identify all four streets because each of the streets had one adjacent street with the same length and one with a different length, producing an asymmetric or a one-fold rotationally symmetric environment (Kelly et al., 2008). When there was no street configuration cue, the streets described above were substituted by four identical streets, the total length of which is equal to that of the original streets.



Figure 2.1. An example of the experimental environments (bird's eye view).

The experimental design was comprised of a combination of learning cue groups and different testing cue types (Figure 2.2). The learning cue group was manipulated between participants with two conditions: A competition group in which both the building and the street configuration cue were presented during learning and a no-competition group in which the type of cues presented during learning was the same as that presented during testing. The testing cue type was manipulated within participants with four conditions: B-test-trials in which only the building cue was presented during testing, S-test-trials in which only the street configuration cue was presented during testing, SB-test-trials in which both cues were presented during testing, and Conflict-test-trials in which both cues were presented during testing but the building and the street configuration were displaced relative to each other to indicate a conflicting orientation. Note that in the Conflict-test-trials, the building and the street configuration were displaced such that the response street indicated by the building and the response street indicated by the street configuration had the same length to prevent participants from using one single street length as a cue (see Figure 2.2).



Figure 2.2. Examples of the experimental conditions of Experiments 1 and 2.  $\otimes$  denotes the building. Four objects were located at the end of the four streets respectively. X denotes the original location of one target object. At learning, participants were transported to each object at a constant speed by the computer. At testing, participants were released at the center of the intersection and were asked to choose between the two streets denoted by X and Y. X and Y had the same length. When four streets had the same lengths during testing in the B-test-trials, X and Y had the same angular distance from the building, i.e., both closer to the building or both farther away from the building.

More specifically, in the competition group, the learning cues were always SB, and the testing cues could be S, B, SB, or conflicting SB. In the no-competition group, the learning cues could be S, B, or SB, and the testing cues were the same as the learning cue (S, B, or SB), except that in the conflict-test-trials, the learning cues were SB and the testing cues were conflicting SB. The learning cue groups were so named because on the S-test-trials and the B-test-trials, participants in the competition group learned two cues that might compete with each other, but participants in the no-competition group only learned a single cue removing the potential competition. The distinction between competition and no-competition is nominal for the SB-test-trials.

Participants were randomly assigned to the two groups subject to the constraint that there were an equal number of males and females in each group. There were 16 trials for each participant. The first twelve trials were randomly assigned to the B-test-, S-test-, and SB-testtrials, four trials for each. The last four trials were the Conflict trials. The reason the Conflict trials were last was that participants may have decided that the cues were unreliable if they found the cues were in conflict, and this might have affected their performance in the other conditions in an unpredictable way.

For the test phase of each trial, participants judged the locations of two objects. Specifically, they localized the first and third objects that they had learned. It is important to note that these two objects were originally located at the opposite streets so that the two target streets were different in terms of street length (short vs. long) and their angular distance with the building (closer vs. farther). For each target object, participants chose between the correct street and one distracting street. In all types of trials, the distracting street and the correct

street had the same length. In the B-test-trials, in which all four streets during testing had the same length, the distracting street and the correct street had the same angular distance with the building (i.e., both closer to or both farther away from the building).

### 2.3.2 Procedure

Wearing a blindfold, participants were guided into the testing room and seated on the swivel chair. Participants donned the HMD and then removed the blindfold. Participants were instructed to pretend to be passengers who would travel a city in a car. Participants were always passively transported. They never physically locomoted during transportation but they could physically turn their head to have a viewpoint different from their travelling direction.

In the learning phase of each trial, participants were transported at a constant speed (10 m/s for translation and 45% for rotation) from the center of the intersection to the end of each street. Fog was placed in front of participants with a distance (15 m) so that participants could not see the ends of streets when they stood at the intersection. If participants could have seen the ends of the streets at the intersection, they might have easily identified all objects without any navigation. At the end of each street they could see an object and were instructed to learn its location. Then they were transported back to the center of the intersection before visiting the next object at the end of the adjacent street (clockwise or counter-clockwise). The first object that they visited and the learning order (clockwise or counter-clockwise) were randomized. Participants' initial orientation was aligned with their travelling direction. Participants could look around during their movement.

After all objects were visited once, all objects were removed and the screen turned black for two seconds. Then the testing phase started. No fog was placed to block

participants' view of either the street configuration or the building. The specific cues (the street configuration, the building or both) were presented. Participants were released at the center of the intersection with a random orientation. An object was shown at the right bottom corner of the screen and participants were instructed to choose the correct street for that object using a mouse. They were only allowed to choose between two streets (the correct and the distracting ones). One street was indicated by a green arrow and the other one was indicated by a red arrow. Whether the correct street was indicated by the red or the green arrow was randomized. Participants were asked to click the left mouse button if they chose the street indicated by the red arrow or click the right mouse button if they chose the street indicated by the green arrow. After participants' response, the screen turned black for two seconds. Participants were then released at the center of the intersection with a random orientation and were asked to choose the correct street for the second object. After they had responded for both objects, the screen turned black for two seconds and the next trial began. Participants' responses for both target objects were recorded for each trial.

## 2.3.3 Competition during Encoding

To examine the competition between street configurations and buildings during encoding, we contrasted the competition group with the no-competition group in terms of the accuracy in targets' localization in the B-test-trials and the S-test-trials. Participants in the competition group learned the objects' locations in the presence of both the building and the street configuration, whereas participants in the no-competition group learned the objects' locations in the presence of either the building or the street configuration. If learning the building overshadowed learning the street configuration, then the competition group would perform worse than the no-competition group on the S-test-trials. If learning the street configuration overshadowed learning the building, then the competition group would perform worse on the B-test-trials. If those two cues did not compete with each other, the performance of the competition group and the no-competition group would be comparable on both the Btest-trials and the S-test-trials.

We examine cue interaction during retrieval when the two cues indicated the same orientation and when the two cues indicated different orientations. Below we referred to the former one as Combination during Retrieval and the latter one as Competition during Retrieval. Note that we only examined interaction (combination and competition) during retrieval for the competition group, but not for the no-competition group because the learning conditions in the SB-, S-, and B-test-trials were different in the no-competition group (Mou & Spetch, 2013).

#### 2.3.4 Combination during Retrieval

To examine the combination of cues during retrieval, we contrasted the performance in target localization in the SB-test-trials with the sum of performance in the S-test-trials and in the B-test-trials. If the two cues are combined additively, the performance in the SB-testtrials should be comparable to the sum of the performances in the S-test-trials and in the Btest-trials. Note that a combination model based on variance (e.g. Bayesian combination model reviewed by Cheng et al., 2007) cannot be applied to the current reorientation paradigm because of the nature of the data in the current study. It is difficult to obtain variance in reorientation studies because they usually collect categorical data instead of continuous data.
An accuracy-based combination model. Instead of using variance-based combination models, we developed a combination model based on accuracy, which is the probability of making the correct response. We defined the participants' ability to select the correct response from the alternative response with the presence of valid cues in terms of the logit of the response accuracy. The logit of a probability, p, is defined as logit (p) = log (p/(1-p)). Logit is widely used in modeling binary data. One important advantage of using the logit of accuracy instead of accuracy itself is to address the ceiling effects when accuracies are combined. Specifically, accuracy cannot be larger than 1. The sum of accuracies of S-test-trials and of B-test-trials, however, will be larger than 1 when both cues respectively lead to an accuracy above chance level (i.e., 0.5 as participants chose between two locations). Because the logit can be any real number, it has no ceiling restriction and can be used to model the combination of cues.

The accuracy of localizing the target with the building cue alone is denoted by  $A_B$ . The accuracy of localizing the target with the street configuration cue alone is denoted by  $A_S$ . The accuracy of localizing the target with both cues is denoted as  $A_{SB}$ . If the ability of choosing the correct response due to a single cue (i.e., the building or the street configuration) can be additively combined, then

$$logit (A_{SB}) = logit (A_S) + logit (A_B)$$
(1)

Based on the definition of logit, Equation 1 can also be written as:

$$\frac{A_{SB}}{(1-A_{SB})} = \frac{A_S}{(1-A_S)} * \frac{A_B}{(1-A_B)}$$

Therefore, we obtain

$$A_{SB} = \frac{A_{S^*} A_B}{A_{S^*} A_B + (1 - A_S)^* (1 - A_B)}$$
(2)

Equations 1 and 2 can also be derived from the method described in McClelland (1991, p. 7-8; see also Twilley & Dixon, 2000). (More details are provided in the Appendix.) We contrasted the estimated  $A_{SB}$ , which was calculated based on the observed  $A_S$  and  $A_B$  according to Equation 2, with the observed  $A_{SB}$  to test whether cue combination can be estimated by the proposed accuracy-based combination model.

### 2.3.5 Competition during Retrieval

To investigate the competition between buildings and street configurations during retrieval, we examined the cue preference in the Conflict trials (see Figure 2.2). In each trial, the building was displaced with respect to the street configuration to indicate a conflicting orientation. Participants were then forced to choose between the response indicated by the street configuration (e.g. X in Figure 2.2) and the response indicated by the building (e.g. Y in Figure 2.2).

In the Conflict trials, the tendency to select the response indicated by one cue is compromised by the tendency to select the response indicated by the other cue. Therefore, the probability of choosing the response indicated by one cue (e.g. the street configuration) should be determined by subtracting the tendency to select the response indicated by the other cue (e.g. the building) from the tendency to select the response indicated by this cue (e.g. the street configuration).

We denote the probability of choosing the response indicated by the street configuration in the Conflict trials as  $P_{S|Conflict}^2$ . Formally, we produce the following equation:

<sup>&</sup>lt;sup>2</sup> Whether we use probability of choosing the response indicated by the street configuration or indicated by the building did not rely on any assumption about cue stability and should not

$$logit (P_{S|Conflict}) = logit (A_S) - logit (A_B)$$
(3)

Based on the definition of Logit, Equation 3 can also be written as:

$$\frac{P_{S|Conflict}}{1 - P_{S|Conflict}} = \frac{A_{SB}}{1 - A_S} * \frac{1 - A_B}{A_B}$$

Therefore, we obtain:

$$P_{S|Conflict} = \frac{A_S^{*}(1 - A_B)}{A_S^{*}(1 - A_B) + (1 - A_S)^{*}A_B}$$
(4)

We can derive Equation 4 from Equation 2 directly as well. Participants were forced to choose between the response indicated by the street configuration (e.g. X in Figure 2.2) and the response indicated by the building (e.g. Y in Figure 2.2). The probability of choosing response X using the street configuration cue is still the accuracy in the S-test-trials, i.e.,  $A_s$ . The probability of choosing response X with the displaced building is the error rate in the Btest-trials, i.e., 1-A<sub>B</sub>. Replacing A<sub>B</sub> with 1-A<sub>B</sub> in Equation 2, we still obtain Equation 4.

We contrasted the estimated (or predicted)  $P_{S|Conflict}$ , which was calculated based on the observed  $A_S$  and  $A_B$  according to Equation 4, with the observed  $P_{S|Conflict}$  in the Conflict trials to test whether cue competition in the Conflict trials can be estimated by the proposed accuracy-based combination model. If the observed  $P_{S|Conflict}$  was comparable to the predicted  $P_{S|Conflict}$ , then we would conclude that the cue preference was solely determined by the response accuracy based on individual cues. If the observed  $P_{S|Conflict}$  was larger than the predicted  $P_{S|Conflict}$ , then we would conclude that participants preferred the street configuration more than the preference that is solely determined by the response accuracy using individual cues and the additional preference occurred because participants believed that the street

affect the conclusions about cue preference. We just arbitrarily chose the former one to examine cue preference.

configuration was more stable than the building. If the observed  $P_{S|Conflict}$  was smaller than the predicted  $P_{S|Conflict}$ , then we would conclude that participants preferred the street configuration less than the preference that is solely determined by the response accuracy using individual cues and the lower preference for the street configuration occurred because participants believed that the street was less stable than the building.

#### 2.4 Experiment 1

The purpose of Experiment 1 was to investigate cue interactions between a building and a street configuration during reorientation in a familiar environment. Participants learned the locations of four objects in an intersection consisting of a building and four streets (Figure 2.1). The same building was placed on the same corner of the same layout of streets across trials, allowing participants to become familiar with that environment.

We hypothesized that, in a familiar environment, participants encoded the relations between the building and the street configuration. The represented relations between the building and the street configuration could reduce the competition between these two cues during encoding. The represented relations between the building and the street configuration could also be used to detect the relative displacement between the building and the street configuration. Therefore, participants might choose the cue that they believed to be more stable with a probability higher than what is solely determined by response accuracy using individual cues.

# 2.4.1 Method

**Participants.** Ninety-six university students (48 men and 48 women) participated in this experiment as partial fulfillment of a requirement in an introductory psychology course.

**Materials, design, and procedure.** In addition to the materials, design, and procedure described in the General Method above, the appearance of the building and the street configuration were the same across the learning phases of all the 16 trials. The relationship between the building and the street configuration were also constant across all the trials: the building was always located between the two short streets. The building was approximately 10 m long, 10 m wide and 50 m tall. The street configuration consisted of two long streets (50 m each) and two short streets (25 m each). When there was no street configuration cue, the street configuration cue was substituted by four 37.5 m-long identical streets.

# 2.4.2 Results and Discussion

**Competition during encoding.** Figure 2.3 plots the mean accuracy as a function of testing cue type (S-, B-, SB-test-trials) and learning cue group (competition or nocompetition). Accuracy was computed for each participant and each testing cue type condition (S-, B-, SB-test-trials), and analyzed in mixed-model analyses of variance (ANOVAs), with variables corresponding to testing cue type (within participants) and learning cue group (between participants).

The main effect of testing cue type was significant, F(2,188) = 6.06, p < .01, MSE = 0.026,  $y_p^2 = 0.06$ . The main effect of learning cue group was not significant, F(1,94) = 0.17, p = 0.68, MSE = 0.072,  $y_p^2 = 0.002$ . The interaction between testing cue type and learning cue group was not significant, F(2,188) = 0.40, p = 0.67, MSE = 0.026,  $y_p^2 = 0.004$ . The null effect of learning cue group and the null interaction between testing cue type and learning cue

group suggest that learning the buildings and learning the street configurations did not compete with each other.



Figure 2.3. Proportion correct in locating target objects as a function of testing cue type and learning cue group in Experiment 1. Error bars represent standard errors of the mean.

The accuracy in all six conditions (combinations of the two independent variables) was above chance level (ts (47) > 2.78, ps < .01). The performance in the S-test-trials was significantly worse than that in the SB-test-trials (t(188) = 3.47, p < .001). The performance in the B-test-trial was significantly different from that in the S-test-trials (t(188) = 2.01, p = 0.04)<sup>3</sup> but was not different from the SB-test-trials (t(188) = 1.45, p = 0.15). The result

<sup>&</sup>lt;sup>3</sup> There are different approaches of post-hoc comparison including Fisher's LSD test and the Bonferroni correction. We used Fisher's LSD test to conduct the post-hoc comparison and let readers decide how to interpret the statistical results. The Bonferroni correction can be implemented by using an alpha of .05/3 in this case.

shows that reorientation using the building was more accurate than using the street configuration.

**Combination during retrieval.** Equation 2 was used to test whether these two cues were additively combined in the SB-test-trials in the competition group. The estimated  $A_{SB}$  was computed for each participant using Equation 2. The means of the estimated  $A_{SB}$  and of the observed  $A_{SB}$  across participants are plotted in Figure 2.4. They were not significantly different from each other (t(47) = 0.02, p = 0.98). This result was consistent with the conclusion that those two cues were combined additively during testing.



Figure 2.4. Observed and estimated proportion correct in locating target objects when both buildings and street configurations indicated the same orientation ( $A_{SB}$ ) in the competition group in Experiment 1. Error bars represent standard errors of the mean.

**Competition during retrieval.** Equation 4 was used to investigate whether participants preferred cues solely according to response accuracy based on individual cues in the Conflict trials. The means of the observed  $P_{S|Conflict}$  and the estimated  $P_{S|Conflict}$  based on Equation 4 across participants are plotted in Figure 2.5. The former was significantly larger than the latter (t(47) = 2.96, p < .01). Therefore, the percentage of actually choosing the street indicated by the street configuration was significantly higher than what was estimated based on the relative response accuracy using each cue. This result suggested that participants might have believed that the street configuration was more stable than the building, consistent with our speculation that a larger item is believed to be more stable.



Figure 2.5. The observed and estimated percentage of choosing the response location indicated by the street configuration when the building and the street configuration were in conflict ( $P_{S|Conflict}$ ) in the competition group in Experiment 1. Error bars represent standard errors of the mean.

#### 2.5 Experiment 2

The purpose of Experiment 2 was to investigate the interactions of buildings and street configurations during reorientation in an unfamiliar environment. Unlike Experiment 1, in which we used the same building and set of streets across trials, we used 16 different combinations of four different buildings and four sets of streets in Experiment 2. As the environment (i.e., the combination between buildings and street configurations) changed from trial to trial, participants experienced a novel environment on every trial.

We hypothesized that, in an unfamiliar environment, participants would not accurately encode the relations between the building and the street configuration. Hence, no mental representation of the spatial relations between the building and the street configuration could be used to reduce the competition between these two cues during encoding. Consequently, cue competition between these two cues during encoding was expected to be observed. Similarly, no represented spatial relations between the building and the street configuration could be used to detect the relative displacement between the street configuration and the building. Therefore, participants' preference of cues was totally determined by the relative response accuracy using each cue during the test in the Conflict trials.

#### 2.5.1 Method

**Participants.** Ninety-six university students (48 men and 48 women) participated in this experiment as partial fulfillment of a requirement in an introductory psychology course.

**Materials and design.** The material and design in Experiment 2 was the same as in Experiment 1 except for the following change. In Experiment 2, the virtual environment in

each trial was novel. We used four different buildings and four street configurations with different length ratios of the short street to the long street (1:2, 1:2.5, 1:3, and 1:3.5) keeping the sum of the short and long streets were 75 m (25:50, 21:54, 19:56, and 17:58). Thus, we created 16 different environments (combinations of four buildings and four street configurations). We assigned each environment to one of the 16 trials so that environments in all the 16 trials were different. Furthermore, the location of the building with respect to the streets was randomized for each configuration. The 16 environments were randomly assigned into the four types of trials with the restriction that each length ratio was used once in each type of trials.

# 2.5.2 Results and Discussion

**Competition during encoding.** Mean accuracy as a function of testing cue type (S-, B-, SB-test-trials) and learning cue group is plotted in Figure 2.6. Accuracy was computed for each participant and each testing cue type condition (S-, B-, SB-test-trials) and analyzed in mixed-model analyses of variance (ANOVAs), with variables corresponding to testing cue type (within participants) and learning cue group (between participants).

The main effect of testing cue type was significant, F(2,188) = 3.61, p < .05, MSE = 0.035,  $y_p^2 = 0.04$ . The main effect of learning cue group was significant, F(1,94) = 5.20, p < .05, MSE = 0.05,  $y_p^2 = 0.05$ . The interaction between testing cue type and learning cue group was not significant, F(2,188) = 0.80, p = 0.45, MSE = 0.035,  $y_p^2 = 0.008$ . The effect of learning cue group together with the null interaction between testing cue type and learning cue group indicates that learning the buildings and learning the street configurations competed with each other during encoding. The null interaction between testing cue type and

learning cue group might indicate that the overshadowing effects carried over to the SBtesting trials although SB-testing trials were the same in these two groups. Another explanation is that participants in the competition group could not predict whether both cues were available during test but those in the no-competition group could in the testing phase of the SB-testing trials.



Figure 2.6. Proportion correct in locating target objects as a function of testing cue type and learning cue group in Experiment 2. Error bars represent standard errors of the mean.

trials was not significant (t(188) = 1.64, p = 0.10). The performance in the S-test-trials was significantly worse than that in the SB-test-trials (t(188) = 2.65, p = .008).

**Combination during retrieval.** Equation 2 was used to test whether these two cues were additively combined in the SB-test-trials in the competition group. The means of the estimated  $A_{SB}$  and of the observed  $A_{SB}$  across participants are plotted in Figure 2.7. They were not significantly different from each other (t(47) = 0.56, p = 0.58). This result indicated that those two cues were combined additively during testing.



Figure 2.7. Observed and estimated proportion correct in locating target objects when both buildings and street configurations were presented (A<sub>SB</sub>) in the competition group in Experiment 2. Error bars represent standard errors of the mean.

**Competition during Retrieval.** Equation 4 was used to investigate whether participants preferred cues solely according to response accuracy based on individual cues in the Conflict trials. Figure 2.8 plots the mean of the  $P_{S|Conflict}$  estimated based on Equation 4 and the observed  $P_{S|Conflict}$  across participants. The former was not significantly different from the latter (t(47) = 0.85, p = 0.40). This result suggested that the percentage of actually choosing the location indicated by the street configuration was comparable to what was estimated based on the relative response accuracy based on each cue alone.



Figure 2.8. The observed and estimated percentage of choosing the response location indicated by the street configuration when the building and the street configuration were in conflict ( $P_{S|Conflict}$ ) in the competition group in Experiment 2. Error bars represent standard errors of the mean.

### 2.5.3 Model Fit

The results of both experiments showed that the estimated  $A_{SB}$  and the observed  $A_{SB}$ were comparable. Therefore, we concluded that both experiments showed that these two cues were combined additively during testing when these two cues indicated the same response. We acknowledge that this conclusion is based on the null effect of contrasting the estimated  $A_{SB}$  and the observed  $A_{SB}$ . In order to strengthen the evidence for the additive combination of cues, we compared three different models of the results from S-test-trials, B-test-trials, and SB-test-trials in the competition groups. Because both experiments showed the null effect, we combined the data from the two experiments.

In the additive model, we assumed that performance (in terms of log odds accuracy or logit) was based on the response strength for street configurations and the response strength for the buildings. In particular,  $logit(A_S) = R_S$ ,  $logit(A_B) = R_B$ , and  $logit(A_{SB}) = R_S + R_B$ . In a full model, we assumed that performance in the SB-test-trials was unconstrained; thus, log odds accuracy would be determined by a separate response strength parameter in each testing cue type. In particular,  $logit(A_S) = R_S$ ,  $logit(A_B) = R_B$ , and  $logit(A_{SB}) = R_{SB}$ . Finally, we also considered a model in which participants simply selected the best cue for the SB-test-trials, which, in these experiments, was the building. In this case,  $logit(A_S) = R_S$ ,  $logit(A_B) = R_B$ , and  $logit(A_{SB}) = R_S$ ,  $logit(A_B) = R_B$ , and  $logit(A_S) = R_S$ ,  $logit(A_B) = R_B$ , and  $logit(A_S) = R_S$ ,  $logit(A_B) = R_B$ , and  $logit(A_S) = R_S$ ,  $logit(A_B) = R_B$ , and  $logit(A_S) = R_S$ ,  $logit(A_B) = R_B$ , and  $logit(A_S) = R_S$ ,  $logit(A_B) = R_B$ , and  $logit(A_S) = R_S$ ,  $logit(A_B) = R_B$ , and  $logit(A_S) = R_S$ ,  $logit(A_B) = R_B$ ,  $logit(A_B) = R_S$ ,  $logit(A_B) = R_B$ , and  $logit(A_S) = R_S$ ,  $logit(A_B) = R_B$ .

The models were fit by maximizing the likelihood of the data using the generalized linear modeling program glmer (Bates, Maechler, Bolker, & Walker, 2014) in the statistical environment R (R Core Team, 2015). The fits were compared using the Bayesian Information Criterion (BIC), a common model comparison criterion. The BIC values for the three models were as follows: additive, 1075.0; full, 1080.1; and best cue, 1079.0. By this criterion, the additive model is clearly better than the other two. Following the suggestion of Wagenmakers (2007), the difference in BIC values ( $\Delta$ BIC) can be converted to an approximation of the Bayes factor, ln(Bayes factor) =  $\Delta$ BIC/2. Using this approximation, the Bayes factor for the additive model relative to the full model is 12.81. The Bayes factor for the additive model relative model is 7.39. Typically, these values would be interpreted as positive evidence for the additive model relative to the other two.

## 2.6 General Discussion

This project examined the cue interactions between a building and a street configuration during human adult reorientation in familiar or unfamiliar large-scale environments. There are three important findings: 1) Learning the building and learning the street configuration did not compete with each other in the familiar environment but competed with each other in unfamiliar environments; 2) when the building and the street configuration indicated a consistent orientation during testing, participants additively combined the two cues in both familiar and unfamiliar environments; 3) when the building and the street configuration were displaced relative to each other to indicate a conflicting orientation, participants' cue preference in unfamiliar environments was determined by response accuracy in using these two cues respectively, whereas participants in the familiar environment preferred the street configuration with a probability higher than what was solely based on response accuracy provided by individual cues (equivalently, preferred the building with a probability lower than what was solely based on the response accuracy based on individual cues). The first finding was based on the contrast between the competition group and the nocompetition group. Participants in the competition group saw compound learning cues but a single testing cue, whereas participants in the no-competition group saw the same single cue during learning and testing (the S-test-trials and the B-test-trials in Figure 2.2). Therefore, impaired performance in the competition group would indicate that during the encoding phase, the unused cue, which was presented during learning but removed during testing, overshadowed the used cue, which was presented during both learning and testing. In the familiar environment (Experiment 1), no impaired performance in the competition group was observed (Figure 2.3), indicating that learning the building and learning the street configuration did not overshadow each other. In contrast, in unfamiliar environments (Experiment 2), impaired performance in the competition group was observed whether the single testing cue was the building or the street configuration (S-test-trials and B-test-trials in Figure 2.6), indicating that learning the building and learning the street configuration overshadowed each other.

This finding suggests the familiarity with the environment can affect the competition between buildings and street configurations during encoding. We speculate that the absence of overshadowing in a familiar environment (Experiment 1) might be due to participants' representing the spatial relationship between the building and the street configuration. There are two possible mechanisms in which the represented spatial relation could have reduced or eliminated the overshadowing effect. First, the encoding of the targets' locations in terms of one cue might have facilitated encoding the targets' locations in terms of the other cue. This facilitative effect might have counteracted the overshadowing effect, leading to the null overshadowing effect in the familiar environments. Second, as participants had encoded spatial relations between the building and the street configuration, the cognitive resources that were required to encode spatial relations between the building and the street configuration could have been released. Therefore, participants could have extra cognitive resources to encode their orientation relative to individual cues, reducing or eliminating the cue competition. In the unfamiliar environments, participants might not have encoded the relationship between the building and the street configuration. Therefore, neither mechanisms described above could be used to reduce cue competition. As a result, the overshadowing effect occurred in the unfamiliar environments.

We acknowledge that the early trials in the familiar environment (Experiment 1) might indeed be trials in a novel environment. We removed the first trial of the S-test-trials, the B-test-trials, and the SB-test-trials respectively and only analyzed the other three trials of the S-test-trials, the B-test-trials, and the SB-test-trials in Experiment 1. The same null overshadowing effect was observed (mean accuracy listed in Table 1).

	All trials			Without first trials		
	S	В	SB	S	В	SB
No- competition	0.62	0.65	0.69	0.62	0.64	0.68
Competition	0.59	0.65	0.68	0.61	0.64	0.69

Table 1. Observed mean accuracy as a function of testing cue type (S, B, SB) and competition group with and without removing the first trial in each testing cue type.

The second finding of the current study was that in both familiar and unfamiliar environments, participants additively combined the buildings and the street configurations during judgment. In both experiments, the performance with two consistent testing cues (in the SB-test-trials) was estimated by the accuracy-based combination model. In particular, logit (A<sub>SB</sub>) was equal to the sum of logit(A<sub>S</sub>) and logit(A<sub>B</sub>). Logit of accuracy reflects the ability to distinguish the correct response from the distractor. These results indicated that participants additively combined two individual cues when these two cues indicated the same estimation. This finding is important as it is the first direct empirical indication that two reorientation cues are additively combined during testing. Xu, Regier, and Newcombe (2017) fit a cue combination model with existing empirical data in indoor reorientation, using accuracy response. In their model fit, the response accuracy based on single cue was not empirically obtained but estimated based on their models.

Furthermore, this finding demonstrates a way of examining cue combination using accuracy instead of variance (or standard deviation) of responses. Recently, there has been increasing interest in examining a Bayesian combination in human spatial cognition (Chen & McNamara, 2014; Chen et al., in press; Cheng et al., 2007; Legge et al., 2014; Mou & Spetch, 2013; Nardini et al., 2008; Zhao & Warren, 2015a; see also Huttenlocher et al., 1991). Generally, when a Bayesian combination is analyzed, the variance (or standard deviation) of responses is used. However, in studying human reorientation, the variance (or standard deviation) of responses is hard to observe because participants' responses are usually categorical rather than continuous. Because the method used in the current study examines cue combination using accuracy (Equations 1 and 2, see also McClelland, 1991),

we believe this method provides a powerful tool to study cue combination when participants' responses are categorical rather than continuous. (See alternative methods in Mou & Spetch, 2013; Xu, Regier, & Newcombe, 2017.) We tested the accuracy-based combination model using a recent published study of human indoor reorientation (Du, Spetch, & Spetch, 2016), which is one of few studies that had all requisite conditions (two single cue conditions, both cues condition, and conflict cues condition)<sup>4</sup>. Table 2 summarizes the observed response accuracy in each single cue and both cues condition, and cue preference in the conflict cue condition. The predictions in the both cues and conflict cue conditions based on the accuracy-based combination model are also listed. Clearly, the predicted and observed responses are quite close.

<sup>&</sup>lt;sup>4</sup> We are grateful to one anonymous for the suggestion to apply our model to other published studies.

	(	Observed accuracy			Predicted accuracy	Predicted preference for height
	Height	Distance/ angle	Both cues	Conflict	Both cues	Conflict
Exp 1, height vs. distance	0.84	0.82	0.99	0.55	0.96	0.54
Exp 1, height vs. angle	0.74	0.86	0.97	0.39	0.95	0.32
Exp 2, height vs. distance	0.91	0.88	0.99	0.61	0.99	0.58

Table 2. Observed mean accuracy in single cue and both cues condition, and mean cue preference in the conflict cue condition in Du et al. (2016), and the predictions in the both cues and conflict cues conditions based on the accuracy-based combination model developed in the current study (Equations 2 and 4).

The third finding of the current study was that when the buildings and the street configurations were in conflict, participants in the unfamiliar environments preferred the cue according to the response accuracy of using individual cues alone, whereas participants in the familiar environments preferred the street configurations with a probability higher than what was predicted by the relative response accuracy using individual cues. As we hypothesized, participants in an unfamiliar environment might not have encoded the spatial relations between the buildings and the street configurations. Without such encoding, they might not have detected changes in the spatial relations between these two cues during the testing phase of the conflicting trials. Therefore, they preferred cues based on response accuracy in single cue trials.

In contrast, participants in the familiar environment might have encoded the spatial relations between the building and the street configuration. Therefore, they might have detected changes in the spatial relations between these two cues during the testing phase of the conflicting trials. Hence, the cue preference was not only determined by the response accuracy using individual cues but also affected by participants' belief on cue stability (Zhao & Warren, 2015b). The higher preference on the street configuration than what was predicted by response accuracy suggested that participants might have believed that the street configuration was more stable, which is consistent with our speculation that a larger item (i.e., the street configuration) seems more stable.

It is important to note that in the current study, we conjectured that cue stability might affect cue preference in the Conflict trials in the familiar environment. However, we did not directly manipulate the relative stability of the cues. The relative stability of the cues was

presumably constant across our manipulations within and between experiments. In the familiar environment (Experiment 1), both the streets and the buildings appeared the same in the learning phases of all the trials in the competition group. Both the street configurations and the buildings changed their appearance, in particular ratio change for street length and disappearing of buildings, in the testing phases of only the single cue trials (B- or S-testtrials) in the competition group. In Experiment 2, in addition to the appearance changes across learning and testing phases like in Experiment 1, both the street configurations and the buildings also varied across different trials, in particular four different configurations associated with four different buildings. Therefore, we did not purposely increase the relative stability of the street configuration in the familiar environments or decrease the relative stability of the street configuration cues in the unfamiliar environments. Future research is needed to directly manipulate cue stability and test whether the discrepancy in cue preference between familiar and unfamiliar environments was really caused by participants' belief of cue stability.

To explain both the null overshadowing effect and the additive cue effects in the familiar environment (Experiment 1), we speculate that participants should have encoded the spatial relations between cues as well as the spatial relations between individual cues and the targets. But could these findings be interpreted by a gestalt-type representation of the environment? In a gestalt-type representation, every target is encoded with respect to the entire environment; there is no independent representation of the relations between the target and any individual cues in the environment. Mou and Spetch (2013, Experiment 5) demonstrated that if participants developed a gestalt-type representation of an array of objects

(a shape formed by cue objects and the target object), there were both overshadowing effects and super-additive cue effects. These demonstrations suggest that the findings of Experiment 1 may not be explained by a gestalt-type representation of the environment. We note that we cannot exclude that possibility that people develop a gestalt-type representation if they overlearn an environment.

All these findings support our proposal that in studying cue interaction, we should examine cue competition during both encoding and retrieval phases and cue combination in the retrieval phase. Whether we study cue competition in the encoding or in the retrieval phases may change our conclusion on relative importance of cues. For example, the null overshadowing effect in Experiment 1 indicated that neither the building nor the street configuration was more important in using cognitive resources during encoding orientation in terms of cues. Otherwise, one may overshadow the other one. However, participants in the same experiment preferred the street configuration in the retrieval phase when these two cues indicated different orientations, indicating that the street configuration might be dominant in the retrieval phase. In addition, whether we study cue competition or cue combination in the retrieval phase might also change our conclusion on cue importance. For example, in Experiment 1, participants additively combined the cues of the building and the street configuration when they indicated the same orientation, which suggested that the building (the cue producing more accurate responses) had a larger contribution to the combined estimation. However, when these two cues indicated different orientations, participants preferred the street configuration cue over the building cue. Hence, it is important to examine

all these three types of cue interaction in the same experiment in order to get an accurate picture of cue interaction in all spatial behaviors.

Most importantly, the findings of the current study indicate that familiarity with the environment modulated cue competition in encoding and retrieving the orientations. These findings suggest that we should consider the role of familiarity with the environment when we study cue interaction during reorientation or in other spatial tasks.

# 2.7 Appendix

Proof of

$$A_{SB} = \frac{A_S * A_B}{A_S * A_B + (1 - A_S) * (1 - A_B)}$$

We assume that each of the two responses can be characterized by response strength. Using the Luce (1963) choice model, the probability of being correct, A, and incorrect, I - A, would be:

$$A = \frac{X}{X+Y}$$
$$1 - A = \frac{Y}{X+Y}$$

where *X* and *Y* are the response strengths for the correct and incorrect response. McClelland (1991) argued (following Morton, 1969; see also Ashby & Townsend, 1986) that the response strengths for independent cues should multiply. Thus,  $X_{SB} = X_S X_B$  and  $Y_{SB} = Y_S Y_B$  where  $X_{SB}$  and  $Y_{SB}$  are the response strengths when both street configuration and building are available,  $X_S$  and  $Y_S$  are the response strengths when only the street configuration is available, and  $X_B$  and  $Y_B$  are the response strengths when only the building is available. Algebraic manipulation yields:

$$A_{SB} = \frac{X_{SB}}{X_{SB} + Y_{SB}} = \frac{X_S X_B}{X_S X_B + Y_S Y_B} = \frac{\frac{X_S X_B}{(X_S + Y_S)(X_B + Y_B)}}{\frac{X_S X_B}{(X_S + Y_S)(X_B + Y_B)} + \frac{Y_S Y_B}{(X_S + Y_S)(X_B + Y_B)}}$$
$$= \frac{\frac{X_S}{(X_S + Y_S)} * \frac{X_B}{(X_S + Y_S)} * \frac{X_B}{(X_B + Y_B)}}{\frac{X_S}{(X_S + Y_S)} * \frac{X_B}{(X_B + Y_B)} + \frac{Y_S}{(X_S + Y_S)} * \frac{Y_B}{(X_B + Y_B)}}$$
$$= \frac{A_S * A_B}{A_S * A_B + (1 - A_S) * (1 - A_B)}$$

### 2.8 References

- Ashby, F. G., & Townsend, J. T. (1986). Varieties of perceptual independence. *Psychological Review*, 93(2), 154–179.
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014). *Ime4: Linear mixed-effects models using Eigen and S4*. R package version 1.1-7, http://CRAN.R-project.org/package=lme4.
- Brown, A. A., Spetch, M. L., & Hurd, P. L. (2007). Growing in circles rearing environment alters spatial navigation in fish. *Psychological Science*, *18*(7), 569-573.
- Chen, X., & McNamara, T. P. (2014). Bayesian cue interaction in human spatial navigation.
  In C. Freksa, B. Nebel, M. Hegarty, & T. Barkowsky (Eds.), *Spatial cognition IX* (pp. 147-160). Springer International Publishing.
- Chen, X., McNamara, T. P., Kelly, J. W., & Wolbers, T. (2017). Cue combination in human spatial navigation. *Cognitive Psychology*, *95*, 105–144.
- Cheng, K. (1986). A purely geometric module in the rat's spatial representation. *Cognition,* 23(2), 149-178.
- 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 & Review*, 20(6), 1033-1054.
- Cheng, K., Shettleworth, S. J., Huttenlocher, J., & Rieser, J. J. (2007). Bayesian integration of spatial information. *Psychological Bulletin*, *133*(4), 625.

- 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.
- Du, Y., Spetch, M. L., & Mou, W. (2016). Look up: Human adults use vertical height cues in reorientation. *Memory & Cognition*, 44, 1277-1287.
- Etienne, A. S., & Jeffery, K. J. (2004). Path integration in mammals. *Hippocampus*, 14(2), 180-192.
- Foo, P., Warren, W. H., Duchon, A., & Tarr, M. J. (2005). Do humans integrate routes into a cognitive map? Map-versus landmark-based navigation of novel shortcuts. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 31*(2), 195-215.
- Gray, E. R., Bloomfield, L. L., Ferrey, A., Spetch, M. L., & Sturdy, C. B. (2005). Spatial encoding in mountain chickadees: Features overshadow geometry. *Biology Letters*, 1, 314–317.
- Hermer, L., & Spelke, E. S. (1994). A geometric process for spatial reorientation in young children. *Nature*, *370*, 57–59.
- Hermer, L., & Spelke, E. (1996). Modularity and development: The case of spatial reorientation. *Cognition, 61,* 195–232.
- Holden, M. P., Newcombe, N. S., & Shipley, T. F. (2013). Location memory in the real world: Category adjustment effects in 3-dimensional space. *Cognition*, *128*(1), 45-55.
- Huttenlocher, J., Hedges, L. V., & Duncan, S. (1991). Categories and particulars: Prototype effects in establishing spatial location. *Psychological Review*, *98*, 352–376.

- Kelly, J. W., McNamara, T. P., Bodenheimer, B., Carr, T. H., & Rieser, J. J. (2008). The shape of human navigation: How environmental geometry is used in maintenance of spatial orientation. *Cognition*, 109(2), 281-286.
- 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.
- Lee, S. A., & Spelke, E. S. (2010). A modular geometric mechanism for reorientation in children. *Cognitive Psychology*, 61(2), 152-176.
- Legge, E. L., Wystrach, A., Spetch, M. L., & Cheng, K. (2014). Combining sky and earth: desert ants (Melophorus bagoti) show weighted integration of celestial and terrestrial cues. *Journal of Experimental Biology*, 217(23), 4159-4166.
- Lew, A. R. (2011). Looking Beyond the Boundaries: Time to Put Landmarks Back on the Cognitive Map? *Psychological Bulletin, 137,* 484-507.
- Lubyk, D.M., Dupuis, B., Gutiérrez, L., & Spetch, M.L. (2012). Geometric orientation by humans: angles weigh in. *Psychonomic Bulletin & Review.* 19: 436-442
- Luce, R. D. (1963). Detection and recognition. In R. D. Luce, R. R. Bush, & E. Galanter (Eds.), *Handbook of mathematical psychology*: Vol. 1 (pp. 103–189). New York: Wiley.
- McClelland, J. L. (1991). Stochastic interactive processes and the effect of context on perception. *Cognitive Psychology*, 23(1), 1-44.
- Montello, D. R. (1993). Scale and multiple psychologies of space. In *Spatial information theory a theoretical basis for GIS* (pp. 312-321). Springer Berlin Heidelberg.

- Morton, J. (1969). Interaction of information in word recognition. *Psychological Review*, 76(2), 165–178.
- Mou, W., Nankoo J., Zhou, R., & Spetch, M. L. (2014). Use of geometric properties for reorientation to remote cities and local objects. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 40,* 476-491
- Mou, W., & Spetch, M.L. (2013) Object location memory: Integration and competition between multiple context objects but not between observers' body and context objects. *Cognition*, 126(2), 181-197.
- 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, 354-367.
- Nardini, M., Jones, P., Bedford, R., & Braddick, O. (2008). Development of cue integration in human navigation. *Current biology*, *18*(9), 689-693.
- Pavlov, I. P. (1927). Conditioned reflexes. New York: Dover.
- 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.
- R Core Team (2015). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.
- Ratliff, K. R., & Newcombe, N. S. (2008). Reorienting when cues conflict: Evidence for an adaptive-combination view. *Psychological Science*, *19*(12), 1301-1307.

- Sampaio, C., & Wang, R.F. (2009). Category-based errors and the accessibility of unbiased spatial memories: A retrieval model. *Journal of Experimental Psychology: Learning, Memory, & Cognition, 35*, 1331-1337.
- Siegel, A. W., & White, S. H. (1975). The development of spatial representations of largescale environments. In H. W. Reese (Ed.), *Advances in child development and behavior*: Vol. 10 (pp. 9-55). Academic Press.
- 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*, 199–210.
- 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 & Review*, 19(2), 270-276.
- Sturz, B. R., & Kelly, D. M. (2013). Environment size and the use of feature and geometric cues for reorientation. *Acta Psychologica*, 142(2), 251-258.
- Twilley, L. C., & Dixon, P. (2000). Meaning resolution processes for words: A parallel independent model. *Psychonomic Bulletin & Review*, 7(1), 49-82.
- Twyman, A., Friedman, A., & Spetch, M. L. (2007). Penetrating the geometric module: Catalyzing children's use of landmarks. *Developmental Psychology*, 43(6), 1523.
- Wagenmakers, E. J. (2007). A practical solution to the pervasive problems of p values. *Psychonomic Bulletin & Review, 14*, 779-804.

- 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. *Learning & Behavior*, 32, 289– 298.
- 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*, 1369–1376.
- Xu, Y. Regier, T., & Newcombe, N. S. (2017). An adaptive cue combination model of human spatial reorientation. *Cognition*, *163*, 56-66.
- Zhao, M., & Warren, W. H. (2015a). How you get there from here: Interaction of visual landmarks and path integration in human navigation. *Psychological Science*, 26(6), 915-924.
- Zhao, M., & Warren, W. H. (2015b). Environmental stability modulates the role of path integration in human navigation. *Cognition*, *142*, 96–109.

# Chapter 3 Effects of Familiarity and Room Size on the Interaction between Geometry and Features during Reorientation

#### 3.1 Abstract

Three experiments investigated the effects of familiarity and room size on the relative use of geometry and features during indoor reorientation. In immersive virtual environments, participants learned objects' locations with respect to room shape and features in a room. The features were isolated objects or wall features. During the test, participants localized objects with room shape only, features only, or both room shape and features. For the trials with both testing cues, the two cues were placed at the original locations or displaced relative to each other during testing. We manipulated room size and participants' familiarity with the environment. In each experiment, participants reoriented themselves in a small room or in a large room. In Experiment 1, participants learned the same cuing objects at the same locations of the same room for all trials (familiar); in Experiment 2, participants learned different cuing objects at different locations of different rooms across trials (unfamiliar); in Experiment 3, participants learned the same wall features at the same locations of the same room for all trials (familiar). There were three important results. First, the room size affected the relative use of geometry and features in familiar rooms but not in unfamiliar rooms. Second, the room size affected the relative use of the cues by modulating the stability of the cues but not the salience of the cues. Third, participants' preference for isolated objects over room shape decreased as room size increased, whereas their preference for wall features over room shape increased as room size increased. Overall, the results showed that both room size and navigators' familiarity with the environments affected the relative use of geometry and features, and the room size effects were modulated by navigators' familiarity with the environments.

#### 3.2 Introduction

When navigators lose track of their orientation, they should reorient themselves using multiple cues in the environment. Those cues include geometric cues and non-geometric features. Geometric cues refer to distance to or geometric relationships among extended surfaces. Non-geometric features include 2D patterns and isolated objects (Lee and Spelke, 2010a). Plenty of studies have investigated the interaction between geometric and featural cues during reorientation (for reviews, see Cheng & Newcombe, 2005; Twyman & Newcombe, 2010; Vallortigara, 2009). One of the most interesting phenomena is that the use of geometry and features is modulated by the size of the environment.

Previous studies of children, fish, and rats found that when both geometry and features are available, the use of features increases as the room size increases. Young children could not use features to reorient in small rooms but could do so in large rooms. Hermer and Spelke (1994, 1996) found that children younger than two years old could only use room shape but not the color of a wall to reorient in a room that was 4 by 6 feet. However, Learmonth, Nadel, and Newcombe (2002) found that children younger than two years old were able to use featural cues, such as a bookshelf placed against a wall or a blue curtain hanging on a wall, to reorient in a room that was 8 by 12 feet.

Sovrano, Bisazzaa, and Vallortigara (2005) found that the relative use of a feature as a beacon increases as the size of an enclosure increases. Fish learned that the location of a target in a rectangular tank consisted of three white walls and one blue wall. The target was at a corner that had a long wall on the left and a short wall on the right. The unique blue wall was on the right of the corner. The authors explained that choosing the corner that was

diagonally opposite to the correct corner would suggest that the fish had successfully used the shape of the tank to identify the two geometrically correct corners but were making errors using the featural cue. If the fish chose the corner adjacent to the correct corner but on the right of the blue wall, they were successfully using the blue wall as a beacon but were making errors using the shape of the tank. The fish were either trained in a small tank and tested in a large tank or trained in a small tank and tested in a large tank. The result showed that the fish made more errors using the geometric cues when transferred from a small to a large space, and made more errors using the featural cues when transferred from a large to a small space. Maes, Fontanari, and Regolin (2009) found similar results with rats looking for a target in a rectangular room that consisted of three black walls and a short wall.

The relative use of geometry and features is also modulated by room size when the two cues are in conflict. Studies on human adults, chicks, and fish (Ratliff & Newcombe, 2008; Sovrano & Vallortigara, 2006; Sovrano, Bisazzaa, & Vallortigara, 2007; but see Lambinet, Wilzeck & Kelly, 2014) found that when room shape and wall features (either a distinctive fabric hanging on the wall or the color of a wall) were in conflict, the probability of choosing the geometrically correct corner was higher in a small room than in a large room, and the probability of choosing the featurally correct corner was higher in a large room than in a small room. Those results suggest navigators assign more weight to featural cues and less weight to geometric cues as room size increases. In sum, all the previous studies showing a room size effect on the interaction between features and geometry suggested that the role of geometry is weakened, and the role of features is strengthened as the environmental size increases.
Although plenty of evidence has been found, the reason for the room size effect on the relative use of geometry and features remains unclear. Moreover, from the previous studies, we could not differentiate whether room size affected the encoding of the cues or the retrieval of the cues, or both. In particular, if room size affected only the encoding of the cues, it would suggest that the features were more used in a large room than in a small room during retrieval because they were better learned in the large room than in the small room. If room size affected only the retrieval of the cues, it would suggest that the features of the cues, it would suggest that in the small room even if the learning was comparable in the large room and in the small room. If room size affected both the encoding and retrieval of the cues, it would suggest that the features were better learned in the large room than in the small room and were more used in the large room than in the small room. However, the improvement during retrieval was greater than the improvement during encoding.

Miller (2009) suggested that room size affects the relative use of geometry and features by affecting the encoding of cues. In an associative model developed by Miller and Shettleworth (2007, 2008), the relative use of cues is determined by the associative strength between each cue and the target, and the increment in associative strength is positively related to the salience of the cue. Miller (2009) speculated that because the relative salience of features increases with room size, the relative use of features increases with room size. To test this hypothesis, he manipulated the salience of featural and geometric cues and simulated the probability of choosing each corner in a room during reorientation using the associative model (Miller & Shettleworth, 2007, 2008). He assigned a greater salience value to the featural cue in a large enclosure than in a small enclosure, and a greater salience value to the

geometric cue in a small enclosure than in a large enclosure, and successfully simulated the room size effect found in previous studies (Chiandetti et al., 2007; Learmonth et al., 2002; Sovrano & Vallortigara, 2006; Vallortigara et al., 2005). However, the successful simulation does not indicate a causal relationship between cue salience and room size. The model itself did not define or independently measure cue salience, and thus could not explain why cue salience should vary with enclosure size.

The salience of features may relate to their size. Gouteux and colleagues (2001) kept the room size constant and changed the size of the featural cues. They found that monkeys were more likely to use featural cues when the cues were larger, and therefore, more salient. In some cases, features in larger enclosures are naturally larger than those in small enclosures. For example, if the featural cue is a colored wall, as the room becomes larger, the colored wall also becomes larger. However, as the enclosure becomes larger, the distance between the colored wall and the navigator also increases. As a result, the colored wall occupies the same retinal area in a small room as in a large room, although its absolute size is bigger in a larger room. Moreover, if the featural cue is an isolated object, its absolute size emains the same, whereas in a larger room where it is farther from the observer, it occupies a smaller retinal area. In other words, if the salience of features increases with enclosure size, it should not be attributed to the increased size of the features.

Sovrano and Vallortigara (2006) speculated that a negative relationship between room size and the salience of geometric cues might have contributed to the room size effect. They suggested that when keeping a certain distance from a corner, navigators can see a larger portion of the room in a small room than in a large room, allowing them to more easily infer the geometric relationships among different parts in a smaller room. This explanation successfully explained the findings in a searching paradigm, in which participants had to search for the target at one of the corners and they were rewarded only when they were close to the corner. If participants only stay at the center of the room and are rewarded with the experimenter's feedback, then the salience of the geometric cue should not differ for the small and large rooms. This hypothesis was supported by Learmonth and colleagues' (2008) finding that young children could use a colored wall to reorient in a large room when they could freely move in the enclosure and search for the target at the corners but could not use the colored wall when their movement was restricted. This result suggests that the featural cue might be overshadowed by the geometric cue that was more salient when the children stayed at the center of the room. When the children could freely move, the salience of the geometric cue decreased in the large room and no longer overshadowed the featural cue. However, Ratliff and Newcombe (2008) found the room size effect during reorientation of human adults even when they were standing at the center of the room pointing to the corner they would search.

The distance of cues have contribute to the room size effect. Sovrano and colleagues (2005) speculated that navigators only use features beyond a certain distance as an orientation cue. Nadel and Hupbach (2006) suggested that a proximal landmark is not preferred as an orientation cue because its orientation with respect to the observer changes rapidly when the observer moves, whereas a distal landmark is a better orientation cue because its orientation remains relatively constant when the observer moves. This assumption was supported by neuroscience studies showing that head direction cells mostly followed distal landmarks

when distal and proximal landmarks were in conflict (Yoganarasimha, Yu, & Knierim, 2006). Unlike isolated features, the geometric shape of a room could indicate orientations with its own frame of reference. Therefore, the orientation indicated by a geometric cue is independent of the observers' movements regardless of the room size. In sum, features are more likely to be used in larger rooms might be because they are more distal and therefore less vulnerable to observers' movements. However, it is not clear whether the distance of features contributes to the room size effect by affecting the encoding or the retrieval of the cues, or both.

Newcombe and Huttenlocher (2006) proposed an adaptive combination theory to explain the interaction between geometry and features during reorientation. They proposed that geometry and features are combined in a Bayesian fashion with their weights determined by cue properties such as salience and stability. This theory is consistent with the room size effect because it predicts that the relative use of cues will vary in different environments. However, to our knowledge, there is no study directly dissociating the roles of salience and stability in the room size effect (i.e., increasing the use of features in a larger room).

In the current study, we conceive of cue salience as an encoding factor. Cue salience determines how many resources participants assign to each cue when encoding their orientation with the presence of both cues. Cue salience can be measured as the response accuracy when only a single cue is available during testing.<sup>5</sup> We conceive of cue stability as a retrieval factor. Cue stability determines, independently of the encoding strength of the cues,

<sup>&</sup>lt;sup>5</sup> Cue salience can also be measured by cue reliability, which is the inverse variance, in a study using a continuous response instead of categorical response (e.g. Chen et al., 2017).

how much weight participants assign to each cue when retrieving their orientation in the presence of two conflicting cues. As cue salience in encoding also contributes to cue preference in retrieval, the effect of cue stability on cue preference is examined by testing whether cue preference can be solely explained by cue salience. If cue preference can be solely explained by cue salience, it would suggest that cue stability has no effect on cue preference during retrieval.

The previous chapter showed that the effects of cue salience and cue stability on cue preference are affected by participants' familiarity. We found that cue salience solely determined cue preference in an unfamiliar environment, whereas both cue salience and cue stability determined cue preference in a familiar environment. Participants in unfamiliar environments were more accurate at reorienting with respect to the buildings and also relied more on the buildings when the buildings conflicted with the street configurations. However, participants in a familiar environment preferred the street configuration when it conflicted with the building although they reoriented more accurately using the building than using the street configuration when only one of the cues was available. We explained that the relative use of cues was only determined by cue salience in unfamiliar environments but was determined by both salience and stability in the familiar environment. This was because people in the familiar environment learned the relationship between the building and the streets and were able to detect whether the cues were in conflict. Then instead of simply relying more on the more salient cue, people should also consider which cue was moved based on the stability of the cues.

The main purpose of this study was to examine the roles of cue salience and cue stability

in the effect of room size on the relative use of geometry and features. First, we examined whether the room size modulated the relative use of geometry and features when the two cues were in conflict. Second, we examined whether the room size modulated the relative salience of geometry and features, which was measured as the relative response accuracy of using each cue. And last, by comparing the effect of the room size on the relative use of cues and on the relative salience of the cues, we could understand whether the former was solely determined by the latter. If the relative salience and the relative use of the features over the geometry changed with the room size in a similar pattern, it would indicate that the room size modulated the relative use of the cues by modulating their relative salience. If the relative use of the features over the geometry changed with the room size, whereas the relative salience of the cues was not affected by the room size, it would indicate that the room size modulated the relative use of the cues by modulating their relative stability but not their relative salience. If both the relative salience and the relative use of the features over the geometry changed with the room size, but in a different pattern, it would indicate that the room size modulated the relative use of the cues by modulating both their relative salience and stability.

In addition, we also tested whether familiarity with the environments could modulate the effect of the room size on the relative use of room shape and features. As we found in Chapter 2, the relative use of cues was solely determined by cue salience in unfamiliar rooms but was determined by both cue salience and stability in familiar rooms. Therefore, if the room size effect is solely due to cue salience, then we should find the room size effect in both familiar and unfamiliar rooms. If the room size effect is solely due to cue stability rooms. If the room size effect in familiar rooms but not in unfamiliar rooms. If the room size

effect is due to both salience and stability, then we should observe the room size effect in both familiar and unfamiliar rooms, but the effect should be stronger in familiar rooms than in unfamiliar rooms.

## 3.3 General method

Three experiments were conducted to examine the role of familiarity and room size in the relative use of room shape and features during reorientation. Experiment 1 tested the relative use of room shape and isolated objects in small and large familiar rooms. Experiment 2 tested the relative use of room shape and isolated objects in small and large unfamiliar rooms. Experiment 3 tested the relative use of room shape and wall features in small and large familiar rooms. The differences in materials, manipulations of familiarity and room size will be discussed in each experiment. Here, we describe the common materials, design, procedure, and the method of data analyses.

#### 3.3.1 Materials and Design

The experiments were conducted in a physical room that was 4 m by 4 m. A swivel chair was placed in the middle of the room. The experiments were implemented in a virtual environment generated using Vizard software (WorldViz, Santa Barbara, CA). The virtual environment was displayed in stereo with an nVisor SX60 head-mounted display (HMD) (NVIS, Inc. Virginia). Each participant was placed in an InterSense IS-900 motion tracking system (InterSense, Inc., Massachusetts) so that participants could look around in the virtual environment. The virtual environment was a room and two identical features. Each participant had 32 trials, each consisting of a learning phase and a testing phase. In the learning phase of each trial, participants learned the location of four target objects (lock,

candle, wood, and bottle) that were located at the four corners of the room. In the testing phase of each trial, participants were required to locate two of the four objects. The locations of the objects differed across trials as in a working memory paradigm (Cheng, 1986).

Participants could rely on two kinds of cues to locate the objects: the room shape, which was a geometric cue; and isolated objects or 2D markings on the wall, which were featural cues. When there were featural cues, they were in front of or on two opposite walls. When there was a geometric cue, the room was a rectangular room consisting of two long walls and two short walls that were 4 m tall. When there was no geometric cue, the room was a square consisting of four identical walls. The area of the rectangular room and the square room was the same within each experiment.

Most of the previous reorientation studies used rectangular rooms that the room shape was symmetric; thus, participants could only differentiate two corners from the other two. However, the featural cue was unique; thus, participants could differentiate all four corners. This design is problematic because the reliability of the cues differs if the probability of predicting the target is different. Unlike the experimental settings in the previous experiments, both the room shape and the features in the current study had the same baseline probability of predicting the target. The geometric cue in the current study was a rectangular room, which is two-fold symmetrical. The featural cues in the current study were two identical landmarks placed in front of two opposite walls, or two identical markings on two opposite walls, respectively. Therefore, both the geometric cue and the featural cues could only predict the target location at a 50% chance level.

The learning phases of all 32 trials were the same. Participants learned the location of four target objects with respect to both the rectangular room and the featural cues. However, we manipulated the cues presented in the testing phase. There were four withinsubject conditions (Figure 3.1): the geometry-only condition, in which only the rectangular room was presented and the features were removed; the feature-only condition, in which the features were presented in a square room; the geometry-and-feature condition, in which both the rectangular room and the features were presented; and the conflict condition, in which both the rectangular room and the features were presented but the features were displaced to the other two walls so that the two cues indicated conflicting orientations. The two single testing cue conditions were used to measure the encoding strength (cue salience). The conflict cue condition was used to measure the cue preference. We could also test whether the observed cue preference could be explained by the cue salience. The geometry-and-feature condition was also included to test whether these two individual cues were combined additively (see the previous chapter).



Figure 3.1. Examples of the within-subject conditions in all the experiments. In Experiment 1 and 2, the features were two identical cuing objects placed in front of two opposite walls, as denoted by the red dots. In Experiment 3, the features were two identical shape on two opposite walls as denoted by the blue bars. Four target objects were located at the four corners respectively. X denotes the location or the equivalent location for one target object.

Each participant located the target objects in each of the four conditions. The first 24 trials were randomly assigned to the geometry-only condition, feature-only condition and geometry-and-feature condition, with eight trials for each. The last eight trials were assigned to the conflict condition. The reason the conflict trials were last was that participants may

have decided that the cues were unreliable if they found the cues were in conflict, and this might have affected their performance in the other conditions in an unpredictable way (Leonard et al., 2018).

For the testing phase of each trial, participants were asked to put two of the four objects back into the original corner. The target objects were chosen at random with the restriction that their locations were not equivalent in terms of their relations to the geometric cue (both had a short wall on the left and a long wall on the right) or the featural cues (both were to the left of the features).

## 3.3.2 Procedure

Wearing a blindfold, participants were guided into the testing room and seated on the swivel chair. Participants donned the HMD and then removed the blindfold. In the learning phase of each trial, participants were released at the center of the virtual room with a random orientation. They were instructed to turn around on the swivel chair to observe the virtual room and learn the locations of four objects which would then be removed and have to be put back. The four target objects were randomly placed at the four corners of the virtual room. The participants were given 20 seconds to learn the layout. After that, all objects were removed, and the screen turned black for two seconds. Then the testing phase started. The specific cues (geometry, features, or both) were presented. Participants were released at the center of the virtual room with a random orientation. An object was shown at the right bottom corner of the screen and participants were instructed to put the object back with a pointer by pointing to the correct corner and clicking a button on the pointer. After the participants responded, the screen turned black for two seconds.

participants was removed. The participants were then released at the center of the virtual room with a random orientation and were asked to put the second object back. After they had responded for both objects, the screen turned black for two seconds and the next trial began. The participants' responses for both target objects were recorded for each trial.

#### 3.3.3 Data Analysis

To investigate whether the room size affects the cue salience of the room shape and the features, we examined the response accuracy of using each single cue in the small rooms and in the large rooms. The cue leading to a higher response accuracy would be the cue with a higher cue salience. If the room size effect was due to cue salience, it would predict a higher response accuracy for the featural cue or a lower response accuracy for the geometric cue in the larger room.

To investigate whether room size affects the relative use of the room shape and the features, we examined the cue preference in the conflict condition in the small rooms and in the large rooms. In each trial of the conflict condition, the features were displaced with respect to the rectangular room to indicate a conflicting orientation. Participants were then forced to choose between the geometrically correct corners and the featurally correct corners. The proportion of choosing the geometrically correct corner (or the proportion of choosing the featurally correct corner) would measure the cue preference. The proportion of choosing the geometrically correct corner. If  $P_{G|Conflict}$  was higher than 0.5, the geometry was the preferred cue. The room size effect in the previous studies (Ratliff & Newcombe, 2008; Sovrano & Vallortigara, 2006; Sovrano, Bisazzaa, & Vallortigara, 2007) predicted a smaller cue preference for the room geometry (i.e.,  $P_{G|Conflict}$ ) in the larger room.

If the room size affected only cue preference but not cue salience, it would be easy to conclude that the room size effect was due to cue stability rather than cue salience. However, if the room size affected both cue preference and cue salience, we would need to determine whether the difference in cue preference was solely determined by the difference in cue salience between the rooms.

Chapter 2 provided a method to estimate cue preference based solely on cue salience.

$$predicted P_{G|Conflict} = \frac{A_G^{*}(1-A_F)}{A_G^{*}(1-A_F) + (1-A_G)^{*}A_F}$$
(1)

The accuracy of localizing the target with geometry only is denoted by  $A_G$ . The accuracy of localizing the target with features only is denoted by  $A_F$ . The predicted probability of choosing the geometrically correct corner is denoted by predicted  $P_{G|Conflict}$ .

By contrasting the difference in the observed  $P_{G|Conflict}$  with the difference in the predicted  $P_{G|Conflict}$  between the rooms, we could determine whether the difference in cue preference was solely determined by the difference in cue salience between the rooms.



Figure 3.2. Three hypothesized results of the experiment. a) If the difference between the cue preferences in the small room and in the large room is comparable to the difference between the relative salience in the small room and in the large room, the room size effect on cue preference can be fully explained by the room size effect on relative salience during encoding. b) If room size affects the cue preference but does not affect the relative salience, the room size effect on cue preference should be attributed to the room size effect on cue weighting during retrieval. c) If room size affects both the cue preferences and the relative salience, salience, but the difference between the cue preferences in the small room and in the large room is different from the difference between the relative salience in the small room and in the large room, the room size effect on cue preference between the relative salience in the small room and in the large room is different from the difference between the relative salience in the small room and in the large room, the room size effect on cue preference should be attributed to the room size effect to the room size effect on cue preference between the relative salience in the small room and in the large room, the room size effect on cue preference should be attributed to the room size effect on the room size effect on the room size effect on cue preference should be attributed to the room size effect on both relative salience during encoding and cue weighting during retrieval.

To examine the combination of cues during retrieval, we contrasted the performance in target localization in the geometry-and-feature condition with the sum of the performance in the geometry-only condition and in the feature-only condition using the following equation:

predicted 
$$A_{GF} = \frac{A_G * A_F}{A_G * A_F + (1 - A_G) * (1 - A_F)}$$
 (2)

The accuracy of localizing the target in the geometry-only condition is denoted by  $A_{G}$ . The accuracy of localizing the target in the features-only condition is denoted by  $A_{F}$ . The accuracy of localizing the target with both cues is denoted as predicted  $A_{GF}$ . Comparable results between the predicted  $A_{GF}$  and the observed accuracy in the geometry-and-feature condition would indicate whether geometry and features were combined additively.

#### 3.4 Experiment 1

The purpose of Experiment 1 was to investigate the relative use of room shape and isolated objects during reorientation in a small or large familiar room. Participants learned the locations of four target objects in a rectangular room with two cuing objects. The same cuing objects were placed at the same location of the room across trials, allowing participants to become familiar with that environment.

We hypothesized that in a familiar environment, participants encoded the relationships between the room and the cuing objects. The represented relationships between the room and the cuing objects could be used to detect the relative displacement between the room and the cuing objects. Therefore, participants might choose the cue that they believed to be more stable with a proportion higher than what was solely determined by response accuracy using individual cues. We also hypothesized that the subjective stability of cues was influenced by the room size. In particular, the subjective stability of the featural cues increased with the size of the room because they become more distal in larger rooms (Nadel & Hupbach, 2006).

3.4.1 Method

**Participants.** Eighty university students (40 men and 40 women) participated in this experiment as partial fulfillment of a requirement in an introductory psychology course.

Materials, design, and procedure. In addition to the materials, design, and procedure described in the General Method above, the room and the cuing objects appeared the same across the learning phases of all 32 trials. The cuing objects were two identical traffic cones. The relationship between the room and the cuing objects was also constant across all the trials during learning: the cuing objects were always located in front of the two long walls. The center of the traffic cones was aligned with the middle of the two long walls and was 50 cm away from the walls. In the conflict condition, the two cuing objects were moved to the front of the two short walls. The center of the traffic cones was 50 cm away from and aligned with the middle of the two short walls.

The participants were randomly assigned to the small room condition and the large room condition. The small room was 4 m by 8 m. When there was no geometric cue, the rectangular room was substituted by a square room (5.66 m by 5.66 m) of the same area. The large room was 12 m by 24 m, which was nine times larger than the small room. When there was no geometric cue, the rectangular room was substituted by a square room (16.97 m by

16.97 m) of the same area. The sizes of the traffic cones were the same in the small or large rooms.

# 3.4.2 Results and Discussion

Mean accuracy as a function of testing cue type (geometry-only, feature-only, geometry-and-feature) and room size (small or large) is plotted in Figure 3.3. Accuracy was computed for each participant and each testing cue type condition (geometry-only, feature-only, geometry-and-feature) and analyzed in mixed-model analyses of variance (ANOVAs), with variables corresponding to testing cue type (within participants) and room size (between participants).

The main effect of the testing cue type was significant, F(2, 156) = 26.00, p < .001,  $MSE = 0.013, y_p^2 = 0.250$ . The main effect of the room size was not significant, F(1, 78) =  $0.013, p = 0.910, MSE = 0.046, y_p^2 < 0.001$ . The interaction between the testing cue type and room size was not significant,  $F(2,156) = 1.219, p = 0.298, MSE = 0.013, y_p^2 = 0.015$ . The null effect of the room size and the null interaction between the testing cue type and room size suggest that changing the room size did not affect the response accuracy of reorientation using geometry or features.



Figure 3.3. Proportion correct in locating target objects as a function of testing cue type and room size in Experiment 1. Error bars represent standard errors of the mean.

The accuracy in all six conditions (combinations of the two independent variables) was above chance level, ts(39) > 8.353, ps < .001. The performance in the geometry-only condition was significantly worse than that in the geometry-and-feature condition, t(79) = -2.687, p = 0.009, Cohen's d = 0.300. The performance in the feature-only condition was significantly worse than that in the geometry-only condition, t(79) = -4.838, p < .001, Cohen's d = 0.541, and in the geometry-and-feature condition, t(79) = -6.027, p < 0.001, Cohen's d = 0.674. The result shows that reorientation was more accurate using the room shape than using the cuing objects, regardless of the room size.

The means of the observed  $P_{G|Conflict}$  (the percentage to choose the corner indicated by the geometry in the conflict conditions) as a function of the room size are plotted in Figure

3.4. The difference between the observed  $P_{G|Conflict}$  in the small room and that in the large room was significant, t(78) = 2.142, p = 0.035, Cohen's d = -0.479.

Equation 1 was used to investigate whether participants preferred cues solely according to response accuracy based on individual cues in the conflict condition. The predicted  $P_{G|Conflict}$  was computed for each participant using Equation 1. The means of the predicted  $P_{G|Conflict}$  as a function of room size are also plotted in Figure 3.4. Consistent with the result that the room size did not affect the response accuracy using individual cues (cue salience), the predicted  $P_{G|Conflict}$  was comparable in different rooms, t(78) = -1.410, p =0.163, Cohen's d = 0.314.

We also conducted mixed-model ANOVAs to examine whether the difference in observed P<sub>G|Conflict</sub> was the same as the difference in the predicted P<sub>G|Conflict</sub>. The main effect of observation-prediction was not significant, F(1, 78) = 0.899, p = 0.346, MSE = 0.068,  $y_p^2 =$ 0.011. The main effect of the room size was not significant, F(1, 78) = 0.587, p = 0.446, MSE= 0.085,  $y_p^2 = 0.007$ . The interaction between observation-prediction and room size was significant, F(1,78) = 7.331, p = 0.008, MSE = 0.068,  $\eta_p^2 = 0.086$ .

A simple effect analysis showed that in the small room, the observed and predicted proportions of choosing the geometrically correct corner were not significantly different, t(39) = -1.260, p = 0.215, Cohen's d = -0.199, although there was a trend that participants chose the geometrically correct corner less often than predicted. However, in the large room, the observed proportions of choosing the geometrically correct corner were significantly higher than predicted, t(39) = 2.553, p = 0.015, Cohen's d = 0.404.



Figure 3.4. The observed and predicted percentage of choosing the response location indicated by the room shape when the room shape and the cuing objects were in conflict  $(P_{G|Conflict})$  as a function of room size in Experiment 1. Error bars represent standard errors of the mean.

Equation 2 was used to test whether the two cues were additively combined in the geometry-and-feature condition. The predicted A<sub>GF</sub> was computed for each participant using Equation 2. The means of the predicted A<sub>GF</sub> and of the observed A<sub>GF</sub> in terms of room size are plotted in Figure 3.5 and analyzed in mixed-model ANOVAs. The main effect of observation-estimation was significant, F(1, 78) = 4.990, p = .028, MSE = 0.009,  $y_p^2 = 0.060$ . The main effect of room size was not significant, F(1, 78) = 0.116, p = 0.734, MSE = 0.033,  $y_p^2 = 0.001$ . The interaction between observation-estimation and room size was not significant, F(1, 78) = 0.009,  $y_p^2 = 0.013$ . These results suggested

that room shape and cuing objects were not additively combined in either the small or large room.



Figure 3.5. Observed and predicted proportion correct in locating target objects when both room shape and cuing objects indicated the same orientation ( $A_{GF}$ ) as a function of room size in Experiment 1. Error bars represent standard errors of the mean.

The results suggest that the room size affected the relative use of the room shape and the cuing objects when the two cues were in conflict but did not affect the relative salience of the room shape and the cuing objects in encoding. Participants were more likely to reorient with respect to the room shape in the large room than in the small room. The result is consistent with our hypothesis that the relative use of the room shape and the isolated objects in familiar environments is not solely determined by the relative salience of the cues. However, the result is inconsistent with previous studies which showed that navigators were more likely to follow featural cues in a larger room. We will address this issue in Experiment 3.

## 3.5 Experiment 2

The purpose of Experiment 2 was to investigate the relative use of room shape and isolated objects during reorientation in a small or large unfamiliar room. Unlike in Experiment 1, in which the appearance of the room, the cuing objects, and their relative locations were the same across trials, we used eight rooms of different sizes and with different colors, and four different cuing objects, and changed the relative location between the rooms and the cuing objects from trial to trial in Experiment 2. As the environment changed from trial to trial, participants experienced a novel environment in every trial.

We hypothesized that in an unfamiliar environment, participants would not accurately encode the relationships between different cues, and thus no represented spatial relationships between the rooms and the cuing objects could be used to detect the relative displacement. Therefore, participants' preferences for cues would be totally determined by the relative response accuracy using each cue in the conflict condition. If, as suggested by the finding in Experiment 1, the room size did not affect the cue salience in the unfamiliar rooms, then the room size would not affect the cue preference in the unfamiliar rooms.

#### 3.5.1 Method

**Participants.** Sixty-eight university students (34 men and 34 women) participated in this experiment as partial fulfillment of a requirement in an introductory psychology course.

Materials, design, and procedure. The material and design in Experiment 2 were the same as in Experiment 1 except for the following change: in Experiment 2, the virtual environment in each trial was novel. For each room size condition, we used four different pairs of cuing objects and eight rooms with different colors and different length ratios of the short walls to the long walls (1:1.5, 1:1.8, 1:2.1, 1:2.4, 1:2.7, 1:3, 1:3.3, 1:3.6), keeping the area of the rooms 32 square meters for the small room condition (4.62 m \* 6.92 m, 4.22 m \* 7.6 m, 3.9 m \* 8.2 m, 3.66 m \* 8.76 m, 3.44 m \* 9.3 m, 3.26 m \* 9.8 m, 3.12 m \* 10.28 m, 2.98 m \* 10.74 m) and 288 square meters for the large room condition (13.86 m \* 20.76 m, 12.66 m \* 22.8 m, 11.7 m \* 24.6 m, 10.98 m \* 26.28 m, 10.32 m \* 27.9 m, 9.78 m \* 29.4 m, 9.36 m \* 30.84 m, 8.96 m \* 32.22 m), the same as in Experiment 1. The cuing objects were two traffic cones, two potted plants, two vases, or two baskets. Thus, we created 32 different environments (combinations of four cuing objects and eight rooms) for each room size condition. We assigned each environment to one of the 32 trials so that environments in all 32 trials were different. Furthermore, the location of the cuing objects with respect to the room was randomly chosen between two options for each trial: the cuing objects were located either in front of the two short walls or in front of the two long walls. The 32 environments were randomly assigned into the four conditions with the restriction that each room was used once in each condition. In the Conflict condition, if the cuing objects were in front of the two short wall during training, they were replaced to the front of the two long walls at test, and vice versa.

#### 3.5.2 Results and Discussion

Mean accuracy as a function of testing cue type (geometry-only, feature-only, geometry-and-feature) and room size (small or large) is plotted in Figure 3.6. Accuracy was computed for each participant and each testing cue type condition (geometry-only, feature-only, geometry-and-feature) and analyzed in mixed-model ANOVAs, with variables corresponding to testing cue type (within participants) and room size (between participants).

The main effect of the testing cue type was significant, F(2, 156) = 32.572, p < .001, MSE = 0.017,  $y_p^2 = 0.295$ . The main effect of the room size was not significant, F(1, 78) = 0.037, p = 0.85, MSE = 0.044,  $y_p^2 < 0.001$ . The interaction between the testing cue type and room size was not significant, F(2,156) = 0.975, p = 0.379, MSE = 0.017,  $y_p^2 = 0.012$ . The null effect of the room size and the null interaction between the testing cue type and room size suggest that changing the room size did not affect the response accuracy of the reorientation using either geometry or features.



Figure 3.6. Proportion correct in locating target objects as a function of testing cue type and room size in Experiment 2. Error bars represent standard errors of the mean.

The accuracy in all six conditions (combinations of the two independent variables) was above chance level, ts(39) > 5.121, ps < .001. The performance in the feature-only condition was significantly worse than that in the geometry-only condition, t(79) = 6.075, p < 0.001, Cohen's d = 0.679, and in the geometry-and-feature condition, t(79) = 6.458, p < 0.001, Cohen's d = 0.722. The latter two did not significantly differ, t(79) = 0.373, p = 0.710, Cohen's d = 0.042. The result shows that reorientation using the room shape was more accurate than that using the cuing objects.

The means of the observed  $P_{G|Conflict}$  (the proportion of choosing the corner indicated by the geometry in the conflict conditions) as a function of the room are plotted in Figure 3.7. The observed  $P_{G|Conflict}$  in the small rooms was not significantly different from that in the large rooms, t(78) = 0.149, p = 0.99, Cohen's d = 0.033.

Equation 1 was used to investigate whether participants preferred cues solely according to response accuracy based on individual cues in the conflict condition. The predicted  $P_{G|Conflict}$  was computed for each participant using Equation 1. The means of the predicted  $P_{G|Conflict}$  as a function of the room size are also plotted in Figure 3.7. Consistent with the result that the room size did not affect the response accuracy using individual cues (cue salience), the predicted  $P_{G|Conflict}$  was comparable in different rooms, t(78) = 0.497, p = 0.621, Cohen's d = 0.111.

We also conducted mixed-model ANOVAs to examine whether the difference in observed  $P_{G|Conflict}$  was the same as the difference in the predicted  $P_{G|Conflict}$ . The main effect of observation-prediction was not significant, F(1, 78) = 1.657, p = 0.202, MSE = 0.080,  $y_p^2 = 0.021$ . The main effect of the room size was not significant, F(1, 78) = 0.214, p = 0.645, MSE = 0.073,  $y_p^2 = 0.003$ . The interaction between the observation-prediction and room size was not significant, F(1, 66) = 0.054, p = 0.817, MSE = 0.080,  $y_p^2 = 0.001$ .



Figure 3.7. The observed and predicted percentage of choosing the response location indicated by the room shape when the room shape and cuing objects were in conflict  $(P_{G|Conflict})$  as a function of the room size in Experiment 2. Error bars represent standard errors of the mean.

Equation 2 was used to test whether the two cues were additively combined in the geometry-and-feature condition. The predicted  $A_{GF}$  was computed for each participant using Equation 2. The means of the predicted  $A_{GF}$  and of the observed  $A_{GF}$  in terms of room size are plotted in Figure 3.8 and analyzed in mixed-model ANOVAs. The main effect of observation-prediction was significant, F(1, 78) = 7.682, p = 0.007, MSE = 0.012,  $\eta_p^2 = 0.090$ . The main effect of the room size was not significant, F(1, 78) < 0.001, p = 1.000, MSE = 0.036,  $\eta_p^2 < 0.001$ . The interaction between observation-estimation and room size was

significant, F(1, 78) = 4.617, p = 0.035, MSE = 0.012,  $y_p^2 = 0.056$ . A simple effect analysis showed that in the small room, the observed accuracy of the geometry-and-feature condition was significantly lower than predicted, t(39) = -3.732, p = 0.001, Cohen's d = -0.590, whereas in the large room, the observed and predicted accuracy of the geometry-and-feature condition was not significantly different, t(39) = -0.414, p = 0.681, Cohen's d = 0.065. The results suggest that the room shape and cuing objects were additively combined in the large room but not in the small room.



Figure 3.8. Observed and predicted proportion correct in locating target objects when both the room shape and cuing objects indicated the same orientation ( $A_{GF}$ ) as a function of the room size in Experiment 2. Error bars represent standard errors of the mean.

Unlike Experiment 1, where the room size affected the participants' relative use of the room shape and isolated objects in retrieval in familiar rooms, the results of Experiment 2 showed that the room size did not affect the participants' relative use of the room shape and isolated objects in retrieval in unfamiliar rooms. Similar as in Experiment 1, the room size did not affect cue salience.

We found a room size effect in Experiment 1 which showed that, participants were more likely to use the geometrical cues and less likely to use the featural cues in the large rooms than in the small rooms when the two cues conflicted. This result is inconsistent with previous studies which found that participants were more likely to use featural cues in larger enclosures (Ratliff & Newcombe, 2008; Sovrano & Vallortigara, 2006; Sovrano, Bisazzaa, & Vallortigara, 2007). The inconsistency could be partially explained by the differences in participants and procedures. First, in many of the previous studies, the participants were young children who may not assign weight to cues based on cue stability. Young children have been found to be unable to properly select stable landmarks during navigation (Heth, Cornell, & Alberts, 1997). In our study, however, the participants were human adults who could understand that the isolated objects were less stable than the room, and therefore may have assigned cue weights accordingly. Second, it is not clear if the participants in the previous studies were familiar with the environment and thus learned the relationships between the cues. If they did not learn the relationships between the cues, they should have assigned weights to the cues based on cue salience instead of stability. Third, most of the previous studies used a searching paradigm that the participants could freely navigate in the environment. In that case, the salience of geometry should have decreased as the enclosure size increased (Sovrano & Vallortigara, 2006), whereas in our study, the participants were

sitting in the center of the room and as a result the salience of geometry should not have been affected by the room size.

The biggest challenge to the reversed room size effect is its inconsistency with the study of Ratliff and Newcombe (2008). In that study, human adults staying at the center of the room and having learned the relationships between the cues also relied more on the featural cue in a large room than in a small room. The primary difference between our study and that of Ratliff and Newcombe (2008) is the featural cues used in the experiments. Ratliff and Newcombe (2008) used a distinct fabric hanging on the wall as the featural cue whereas we used two isolated objects placed on the floor with a certain distance from the wall. As defined by Lee and Spelke (2010a), both 2D patterns and isolated objects are featural cues as opposed to geometric cues, which are extended surfaces. However, little is known about the difference between 2D patterns and isolated objects. The salience and stability of those two kinds of cues might be different. Moreover, they might be affected in different ways by room size, therefore leading to different trends in room size effects. Experiment 3 aimed to address this question by investigating the effect of room size on the relative use of room shape and wall features in familiar environments.

# 3.6 Experiment 3

The purpose of Experiment 3 was to investigate the relative use of room shape and wall features during reorientation in a small or large familiar room. Participants learned the locations of four objects in a rectangular room with two markings on two opposite walls. The same markings were at the same walls across trials, allowing participants to become familiar with that environment. We hypothesized that in a familiar environment, participants encoded the relationships between the room and the wall features. The represented relationships between the room and the wall features could be used to detect the relative displacement between the room and the cuing objects. Therefore, participants might choose the cue that they believed to be more stable with a proportion higher than what was solely determined by response accuracy using individual cues.

#### 3.6.1 Method

**Participants.** Sixty-four university students (32 men and 32 women) participated in this experiment as partial fulfillment of a requirement in an introductory psychology course.

**Materials, design, and procedure.** The materials, design, and procedure in Experiment 3 were the same as in Experiment 1 except that instead of using isolated objects, we used wall features as featural cues. The wall features were two red crosses in the middle of the two long walls. The wall features in the large room were nine times as large as those in the small room so that they occupied the same area of retinal space regardless of room size.

# 3.6.2 Results and Discussion

Mean accuracy as a function of testing cue type (geometry-only, feature-only, geometry-and-feature) and room size (small or large) is plotted in Figure 3.9. Accuracy was computed for each participant and each testing cue type condition (geometry-only, feature-only, geometry-and-feature) and analyzed in mixed-model ANOVAs, with variables corresponding to testing cue type (within participants) and room size (between participants).

The main effect of the testing cue type was significant, F(2, 156) = 7.101, p = .001, MSE = 0.012,  $\eta_p^2 = 0.083$ . The main effect of the room size was not significant, F(1, 78) = 0.208, p = 0.650, MSE = 0.057,  $y_p^2 = 0.003$ . The interaction between the testing cue type and room size was not significant, F(2,156) = 0.048, p = 0.953, MSE = 0.012,  $y_p^2 = 0.001$ . The null effect of the room size and the null interaction between the testing cue type and room size suggest that changing the room size did not affect the participants' response accuracy when reorienting using geometry or features.



Figure 3.9. Proportion of choosing the correct corners as a function of the testing cue type and room size in Experiment 3. Error bars represent standard errors of the mean.

The accuracy in all six conditions (combinations of the two independent variables) was above chance level, ts(39) > 8.895, ps < .001. The performance in the geometry-and-feature condition was significantly better than that in the geometry-only condition, t(79) = 2.958, p = 0.004, Cohen's d = 0.331, and in the feature-only condition, t(79) = 3.715, p < 0.001, Cohen's d = 0.415. The latter two did not significantly differ, t(79) = 0.756, p = 0.452,

Cohen's d = 0.084. The result shows that the accuracy of reorientation was comparable using both the room shape and the wall features.

The means of the observed  $P_{G|Conflict}$  (the percentage to choose the corner indicated by the geometry in the conflict conditions) as a function of the room size are plotted in Figure 3.10. The observed  $P_{G|Conflict}$  was significantly smaller in the small room than in the large room, t(78) = 2.102, p = 0.039, Cohen's d = 0.470.

Equation 1 was used to investigate whether participants preferred cues solely according to response accuracy based on individual cues in the conflict condition. The predicted  $P_{G|Conflict}$  was computed for each participant using Equation 1. The means of the predicted  $P_{G|Conflict}$  as a function of room size are also plotted in Figure 3.10. Consistent with the result that the room size did not affect the response accuracy using individual cues (cue salience), the predicted  $P_{G|Conflict}$  was comparable in different rooms, t(78) = 0.069, p = 0.946, Cohen's d = 0.015.

We also conducted mixed-model ANOVAs to examine whether the difference in the observed  $P_{G|Conflict}$  was the same as the difference in the predicted  $P_{G|Conflict}$ . The main effect of observation-estimation was not significant, F(1, 78) = 2.948, p = 0.090, MSE = 0.061,  $y_p^2 = 0.036$ . The main effect of the room size was not significant, F(1, 78) = 2.082, p = 0.153, MSE = 0.107,  $y_p^2 = 0.026$ . The interaction between observation-prediction and room size was not significant, F(1, 78) = 3.248, p = 0.075, MSE = 0.061,  $y_p^2 = 0.040$ .



Figure 3.10. The observed and predicted percentage of choosing the corners indicated by the room shape when the room shape and the wall features were in conflict ( $P_{G|Conflict}$ ) as a function of room size in Experiment 1. Error bars represent standard errors of the mean.

Equation 2 was used to test whether the two cues were additively combined in the geometry-and-feature condition. The predicted A<sub>GF</sub> was computed for each participant using Equation 2. The means of the predicted A<sub>GF</sub> and of the observed A<sub>GF</sub> in terms of room size are plotted in Figure 3.11 and analyzed in mixed-model ANOVAs. The main effect of observation-estimation was significant, F(1, 78) = 8.500, p = .005, MSE = 0.009,  $\eta_p^2 = 0.098$ . The main effect of the room size was not significant, F(1, 78) = 0.501, p = 0.481, MSE = 0.038,  $\eta_p^2 = 0.006$ . The interaction between observation-estimation and room size was not significant, F(1, 78) = 0.001. These results suggest that

the room shape and wall features were not additively combined in either the small or large rooms.



Figure 3.11. Observed and predicted proportion of choosing the correct corners when both the room shape and wall features indicated the same orientation ( $A_{GF}$ ) as a function of the room size in Experiment 1. Error bars represent standard errors of the mean.

# **3.7 General Discussion**

This study examined the effects of familiarity and room size on the relative use of room shape and isolated objects, and on the relative use of room shape and wall features during reorientation of human adults. There are three important findings. First, room size did not affect the relative salience of the room shape and isolated objects or that of the room shape and wall features regardless of whether participants were familiar or unfamiliar with the rooms. Second, in familiar rooms, the relative use of isolated objects over room shape decreased as the room size increased, whereas the relative use of wall features over the room shape increased as the room size increased when these cues were placed in conflict. Third, the room size did not affect the relative use of the cues in unfamiliar rooms.

First, there was no evidence suggesting that the room size affected the cue salience. We used the response accuracy of using each cue as an indicator of the cue salience. In all the experiments, the response accuracy of using room shape, isolated objects, or wall features in the small rooms was not significantly different from that in the large rooms. Consistently, the predicted  $P_{G|conflict}$  based on the relative response accuracy of using each cue in the small and large rooms was comparable to that in the large rooms. Therefore, the results of the current study did not support a positive relationship between the salience of features and room size (Miller, 2009). Moreover, our results did not support a negative relationship between the salience of geometry and room size (Sovrano & Vallortigara, 2006). Although that proposal is very plausible, it may apply only to a searching paradigm in which navigators can freely navigate rather than stay in the middle of the enclosure.

Note that in Experiments 1 and 2, the large rooms were nine times as big as the small rooms, whereas the size of the isolated cuing objects was the same in the small room and in the large room. In Experiment 3, however, the large rooms were nine times as big as the small rooms, and the wall features in the large rooms were also nine times as big as those in the small rooms so that the wall features occupied the same area of retinal space regardless of room size. This suggests that, at least for human adults, the relative size of features to geometry may not be critical to encoding the cues.
While cue salience during encoding was not sensitive to room size, we did observe that the room size affected cue preference in the familiar rooms. In particular, as the room size increased, the relative use of isolated objects over the room shape decreased, whereas the relative use of wall features over the room shape increased. Our results suggest that these effects of room size were determined solely by cue stability during retrieval.

The positive relationship between room size and the relative use of wall features could be explained by greater usefulness of distal features over proximal features during reorientation (Sovrano et al., 2005; Yoganarasimha, Yu, & Knierim, 2006). Since the wall features are more distal in the large rooms than in the small rooms, the relative use of the wall features should increase in the larger rooms. The result of the current study suggests that the distance of features did not affect cue salience during encoding; rather, it only affected cue stability during retrieval. We speculate that a distal landmark is more stable than a proximal landmark because it is less vulnerable to the observers' movements (Nadel & Hupbach, 2006).

However, the distance of the features is insufficient to explain that the relative use of the isolated objects over the room shape decreased in the larger room. We speculate that cue stability during retrieval could be attributed not only to cue distance but also to the movability of cues. The movability of a cue may be partially determined by the size of the cue. For example, in our study, a small traffic cone is more likely to be moved than a huge room. The movability of a cue may also be determined by how it is connected to other cues. For example, in our study, an isolated traffic cone can easily be moved, whereas moving a wall feature is more difficult because it involves erasing the feature from one wall and painting it on another wall. Moreover, the wall feature may be used to specify the identity of the wall. When we changed a wall feature from one wall to another, it is possible that the participants did not think the feature itself moved, but that the wall with that feature moved. In this case, the movability of a wall feature is equivalent to the movability of the wall having that feature.

In Experiment 1, the traffic cones should be comparably movable in the small and large rooms because their size was the same regardless of the room size. Meanwhile the movability of the room shape should have decreased as room size increased because the large room should be less moveable than the small room. As a result, the relative movability of the room shape decreased with the room size, which led the relative use of the room shape to increase with the room size. Since the movability of the room was remarkably greater than that of the isolated objects, the effect of movability overwhelmed the effect of feature distance on the relative stability of the cues. In Experiment 3, on the other hand, the wall features (or the walls having those features) and the room were scaled with the same ratio. Therefore, the relative movability of the room and the wall features should not have been affected by the room size. In Experiment 3, the room size affected the relative stability of the cues by affecting the distance of the wall features.

In reorientation studies, wall features (such as the color) and isolated objects were commonly used as featural cues to contrast with geometric cues. Wall features and isolated objects were treated as the same type of cues because they were found to be less dominant than the room shape during reorientation (for reviews, see Cheng & Newcombe, 2005; Vallortigara, 2009). Lee and Spelke (2010a) found direct evidence that 2D markings on the wall and isolated objects were not used by children, whereas extended surfaces of similar size and contrast were used by children. Based on those findings, Lee and Spelke (2010b) defined that featural cues are isolated objects or 2D patterns, whereas geometric cues are extended surfaces. However, the different patterns of room size effects found in the current study suggest that it may be important to differentiate wall features and isolated objects in reorientation studies, at least when investigating the room size effect. Previous studies of the room size effect used only wall colors or 2D patterns on the walls as featural cues and showed that the relative use of the featural cues increased with room size (Ratliff & Newcombe, 2008; Sovrano & Vallortigara, 2006; Sovrano, Bisazzaa, & Vallortigara, 2007). We replicated this result using wall features as the featural cues. When we used isolated objects as the featural cues, the room size effect was reversed.

Finally, we found that familiarity affected the room size effect on the relative use of the room shape and isolated objects. The relative use of the room shape and isolated objects was modulated by the room size and was not predicted by the relative salience of the cues in familiar environments, whereas it was not modulated by the room size and was predicted by the relative salience of the cues in unfamiliar environments. This finding is consistent with that in Chapter 2. We speculate that in unfamiliar environments, participants did not learn the relationship between the room shape and the cuing objects, and thus could not detect the conflict between the two cues. Therefore, their preference of the cues was determined by the salience of the cues. However, in familiar environments, the participants learned the relationship between the room shape and the cuing objects. Therefore, they knew the two cues were moved relatively and they had to judge which cue was moved. In this case, their

cue preference was determined not only by the salience of the cues, but also by the stability of the cues.

The familiarity effect on the relative use of cues is consistent with previous findings that cue preference is affected by the subjective discrepancy between the cues. Studies have shown that animals and human adults relied more on a landmark, which was more reliable, when its discrepancy with path integration was small, but relied more on the path integration, which was more stable, when the discrepancy was big (see Cheng et al., 2007 for a review). While a larger physical discrepancy almost certainly leads to a larger subjective discrepancy, increasing familiarity with the environment may also lead to a larger subjective discrepancy. The more familiar the navigators were with the environment, the more capable they were of detecting the discrepancy. Therefore, although the physical discrepancy was the same in the familiar and unfamiliar environments, the subjective discrepancy was larger in the familiar environment than in the unfamiliar environment, which led to a shift in cue preference.

It is worth noting that in children, familiarity may not modulate reorientation because the familiarity effect depends on perceiving the stability of cues. However, young children cannot effectively choose the most useful cue based on cue stability (Heth et al., 1997). Learmonth and colleagues (2008) found children could use a featural cue to reorient if they could physically search the environment but not if their movement was restricted. As demonstrated by Sovrano and Vallortigara (2006), this could be because the salience of the room shape decreased as the room size increased in a searching paradigm but did not vary if the children stayed at the center of the environment. In addition, Learmonth and colleagues found that allowing children to get familiar with a room before their movement was restricted

in the experiment did not increase their probability of using the featural cue, whereas having four trials where they could search in the room increased their probability of using the featural cue in latter trials where their movement was restricted. These results suggest that children's relative use of cues was not affected by their familiarity with the environment but was primarily determined by the perceived cue salience when they were rewarded.

#### 3.8 **References**

- Cheng, K. (1986). A purely geometric module in the rat's spatial representation. *Cognition*, 23(2), 149-178.
- Cheng, K., & Newcombe, N. S. (2005). Is there a geometric module for spatial orientation? Squaring theory and evidence. *Psychonomic Bulletin & Review*, *12*(1), 1–23.
- Chiandetti, C., Regolin, L., Sovrano, V., & Vallortigara, G. (2007). Spatial reorientation: The effects of space size on the encoding of landmark and geometry information. *Animal Cognition*, *10*, 159–168.
- 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.
- Hermer, L., & Spelke, E. S. (1994). A geometric process for spatial reorientation in young children. *Nature*, *370*, 57–59.
- Hermer, L., & Spelke, E. (1996). Modularity and development: The case of spatial reorientation. *Cognition, 61,* 195–232.
- Heth, C. D., Cornell, E. H., & Alberts, D. M. (1997). Differential use of landmarks by 8- and 12-year-old children during route reversal navigation. *Journal of Environmental Psychology*, 17(3), 199–213.
- Lambinet, V., Wilzeck, C., & Kelly, D. M. (2014). Size does not matter, but features do: Clark's nutcrackers (Nucifraga columbiana) weigh features more heavily than geometry in large and small enclosures. *Behavioural Processes*, 102, 3-11.

- Learmonth, A. E., Nadel, L., & Newcombe, N. S. (2002). Children's use of landmarks: Implications for modularity theory. *Psychological Science*, *13*(4), 337–341.
- Lee, S. A., & Spelke, E. S. (2010a). Two systems of spatial representation underlying navigation. *Experimental Brain Research*, 206(2), 179-188.
- Lee, S. A., & Spelke, E. S. (2010b). A modular geometric mechanism for reorientation in children. *Cognitive Psychology*, *61*(2), 152-176.
- Leonard, K., Tian, N., Ivanco, T. L., & Kelly, D. M. (2018). Experience with featural-cue reliability influences featural-and geometric-cue use by mice (Mus musculus). *Journal of Comparative Psychology*, 132(1), 106.
- Maes, J. H. R., Fontanari, L., & Regolin, L. (2009). Spatial reorientation in rats (Rattus norvegicus): Use of geometric and featural information as a function of arena size and feature location. *Behavioural Brain Research*, 201(2), 285–291.
- Miller, N. Y. (2009). Modeling the effects of enclosure size on geometry learning. Behavioural Processes, 80, 306–313.
- 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*, 419–422.
- Nadel, L., & Hupbach, A. (2006). Cross-species comparisons in development: the case of the spatial 'module'. *Attention and performance XXI*, 499-511.
- Newcombe, N. S., & Huttenlocher, J. (2006). Development of spatial cognition. In D. Kuhn & R. S. Siegler (Eds.), *Handbook of child psychology: Cognition, perception, and language*, vol. 2 (6th ed., pp. 734–776). New York: Wiley.

- Ratliff, K. R., & Newcombe, N. S. (2008). Reorienting when cues conflict: Evidence for an adaptive-combination view. *Psychological Science*, *19*(12), 1301-1307.
- Sovrano, V. A., Bisazza, A., & Vallortigara, G. (2005). Animals' use of landmarks and metric information to reorient: Effects of the size of the experimental space. *Cognition*, *97*(2), 121–133.
- Sovrano, V. A., Bisazza, A., & Vallortigara, G. (2007). How fish do geometry in large and in small spaces. *Animal Cognition*, *10*(1), 47–54.
- Sovrano, V. A., & Vallortigara, G. (2006). Dissecting the geometric module. *Psychological Science*, *17*(7), 616-621.
- 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. (2009). Animals as natural geometers. In L. Tommasi, M. A. Peterson, & L. Nadel (Eds.), *Cognitive biology* (pp. 83–104). Cambridge: MIT Press.
- Vallortigara, G., Feruglio, M., & Sovrano, V. A. (2005). Reorientation by geometric and landmark information in environments of different sizes. *Developmental Science*, 8, 393–401.
- Yoganarasimha, D., Yu, X., & Knierim, J. J. (2006). Head direction cell representations maintain internal coherence during conflicting proximal and distal cue rotations:
   Comparison with hippocampal place cells. *Journal of Neuroscience*, *26*(2), 622–631.

# Chapter 4 General Discussion

Navigators could use multiple cues to reorient after they lost track of their orientation. Researchers have defined two types of cues: geometric cues and featural cues. Geometric cues are distance to extended surfaces and featural cues are 2D patterns and isolated objects. Since Cheng (1986) found a dominant role of geometry over features during reorientation, researchers have been interested in the interaction between those two types of cues. Previous studies showed that, although using geometry shows advantages over features in most of the studies, the interaction between them could be affected by many factors. In two studies, my colleagues and I examined the role of familiarity, room size and cue properties in cue interaction during reorientation of human adults.

# 4.1 Review of Experiments

In Chapter 2, we investigated how human adults reorient with buildings and street configurations in a virtual environment. In two experiments, we examined the effect of familiarity on three aspects of interaction between buildings and streets configurations, that are the competition during encoding, the combination during retrieval, and the competition during retrieval. We found that, in the familiar environment, learning streets and buildings did not overshadow each other. The cues were combined additively. When the cues were in conflict, the proportion of choosing the response location indicated by the street configurations was higher than what was predicted by the relative response accuracy using each cue. However, in the unfamiliar environments, learning street configurations and buildings overshadowed each other. The cues were combined additively. When the cues were in conflict, the proportion of choosing the response location indicated by the street configurations was higher than what was predicted by the relative response accuracy using each cue. However, in the unfamiliar environments, learning street configurations and buildings overshadowed each other. The cues were combined additively. When the cues were in conflict, the proportion of choosing the response location indicated by each cue was consistent with what was predicted by the relative response accuracy using each cue. The proportion of choosing the response location indicated by each cue was

results suggested that participants' familiarity with the environment affected cue competition during encoding and retrieval, but did not affect cue combination during retrieval. We concluded that the participants learned the relation between street configurations and buildings in the familiar environment, which counteracted the competition between the cues during encoding. When the cues were in conflict, the relative use of street configurations and buildings was solely determined by cue salience in unfamiliar environments, but was also determined by cue stability in familiar environments where the participants learned the relation between the cues.

In Chapter 3, we investigated how human adults reorient with geometry and features. In Experiment 1 and 2, we examined the effect of room size on the relative use of room shape and isolated objects in familiar and unfamiliar rooms. We found that when the room shape and the isolated objects were in conflict, participants in the familiar rooms relied more on the room shape when the room was larger, which could not be predicted by the relative response accuracy of using each cue. However, in the unfamiliar rooms, the relative use of the room shape and the isolated objects in the small rooms was comparable with that in the large rooms, which was predicted by the relative response accuracy of using each cue. Moreover, in both the familiar and the unfamiliar rooms, the response accuracy of using each cue did not change with room size. Therefore, we concluded that, the room size affected the relative use of the room shape and the isolated objects by modulating cue stability but not cue salience. In Experiment 3, we examined the effect of room size on the relative use of room shape and wall features in familiar rooms. We found that the relative response accuracy of using each cue did not change with room size, whereas the relative response accuracy of using each cue did not change with room size, whereas the relative use of the wall features over the room shape increased when the room was larger. Therefore, we concluded that, the room size affected the relative use of the room shape and the wall features by modulating cue stability, but not through modulating cue salience.

### 4.2 Novel Findings and Implications

The two studies in this dissertation advanced our knowledge of cue interaction during reorientation by showing how familiarity, room size and cue properties affect cue interaction and interact with each other. In this section, I summarized the novel findings of my studies, discussed them in the context of cue interaction and cognitive map and proposed directions for future studies.

# 4.2.1 Familiarity affects cue interaction

In both Chapter 2 and Chapter 3, we found cue interaction was affected by participants' familiarity with the environments. In Chapter 2, learning the street configurations and learning the buildings overshadowed each other in the unfamiliar environments but not in the familiar environment. We speculate that the absence of the overshadowing effect in the familiar environment might be attributed to participants' representation of the spatial relationship between the cues. There are two possible mechanisms in which the represented spatial relation could have reduced or eliminated the overshadowing effect. First, the encoding of the targets' locations in terms of one cue might have facilitated encoding the targets' locations in terms of one cue might have facilitated encoding the targets' locations in terms of the other cue. This facilitative effect might have counteracted the overshadowing effect, leading to the null overshadowing effect in the familiar environments. Second, because the participants had encoded the spatial relation between the cues, the cognitive resources that were required to encode the spatial relation between the cues could

have been released. Therefore, the participants could have extra cognitive resources to encode their orientation relative to the individual cues, reducing or eliminating the cue competition. In the unfamiliar environments, however, the overshadowing effect occurred because the participants might not have encoded the relationship between the cues. Therefore, neither mechanisms described above could be used to reduce cue competition.

In both Chapter 2 and Chapter 3, we found that participants' familiarity with the environments changed the roles of cue salience and cue stability in the relative use of the cues. In the unfamiliar environments, the relative use of the cues when they were in conflict was solely determined by the relative salience of the cues, which was measured as the relative response accuracy of using each cue. However, in the familiar environments, the relative use of the cues when they were in conflict could not be predicted by the relative cue salience. As we hypothesized, participants in the unfamiliar environments might not have encoded the spatial relation between the cues, without which they might not have detected that the spatial relation between the two cues was changed. Therefore, their cue preference was determined by the relative response accuracy of using each cue. In contrast, participants in the familiar environments might have encoded the spatial relation between the cues, which was changed. Hence, their cue preference was not only determined by the response accuracy of using individual cues but was also affected by participants' belief on cue stability (Zhao & Warren, 2015a).

Cheng and colleagues (2007) proposed that, when multiple cues were in conflict, cue preference would be affected by the subjective discrepancy between the cues (see also, Cheng, 1994; Cheng, 1995). Empirical studies have showed that, when landmarks and path integration were in conflict, animals' and human adults' preference of the cues was determined by the physical discrepancy between the cues. When the physical discrepancy was small, they relied more on the landmarks because their spatial localization using the landmarks was more accurate (less variable) than using the path integration. However, when the physical discrepancy was large, they relied more on the path integration because they judged that the landmarks were moved and should not be trusted (Etienne, Teroni, Portenier, & Hurni, 1990; Foo et al., 2005; Shettleworth & Sutton, 2005; Zhao & Warren, 2015b). While a larger physical discrepancy should certainly lead to a larger subjective discrepancy, increasing familiarity with the environment may also lead to a larger subjective discrepancy. The more familiar navigators were with the environment, the more capable they were of detecting the discrepancy. In Chapter 2 and Chapter 3, although the physical discrepancy was the same in the familiar and the unfamiliar environments, the subjective discrepancy was larger in the familiar environment than in the unfamiliar environment, which led to a shift in the strategies of cue selection.

# 4.2.2 Room size affects the relative use of cues by modulating cue stability but not salience

We investigated how room size affects the relative use of cues in Chapter 3. We found that when the cues were in conflict, the relative use of the isolated objects over the room shape decreased as the room was larger, whereas the relative use of the wall features over the room shape increased as the room was larger. Although the trends of the effects were different, the common finding was that both the effects were not predicted by the relative salience of the cues, which was measured as the relative response accuracy of using each cue. In all the experiments in Chapter 3, the response accuracy of using each cue in the small rooms was not significantly different from that in the large rooms. Moreover, the predicted probability of choosing the geometrically correct or featural correct corners based on the relative response accuracy of using each cue was not significantly different in terms of room size.

The result of Chapter 3 contradicted the assumption that featural cues are more salient or geometric cues are less salient in larger rooms (Miller, 2009). In Experiment 1 of Chapter 3, the large rooms were 9 times as big as the small rooms and the isolated objects were the same size in both small and large rooms. In Experiment 3 of Chapter 3, the large rooms were 9 times as big as the small rooms and the wall features in the large rooms were also 9 times as big as those in the small rooms. Therefore, the wall features occupied the same area of retinal space, and the same proportion of the room in the small and large rooms. In both experiments, the results did not support a positive relation between the salience of features and room size regardless of the size of the featural cues. A negative relation between the salience of geometry and room size, although very plausible, may only apply to a searching paradigm when navigators could freely navigate rather than staying in the middle of the enclosure (Sovrano & Vallortigara, 2006).

Despite the insensitivity of cue salience to room size, we did find the relative use of the cues to be modulated by the room size. In Experiment 1 of Chapter 3, the relative use of the isolated objects over the room shape decreased as the room size increased. In Experiment 3 of Chapter 3, the relative use of the wall features over the room shape increased as the room

size increased. Since those effects of room size could not be explained by cue salience during encoding, they could only be attributed to cue stability during retrieval.

We speculate that, there were two factors that contributed to the cue stability during retrieval. Firstly, a distal feature is more stable than a proximal feature. The orientation of a proximal landmark with respect to an observer changes rapidly when the observer moves, whereas the orientation of a distal landmark remains stable when the observer moves (Nadel & Hupbach, 2006; Sovrano et al., 2005; Yoganarasimha, Yu, & Knierim, 2006). Secondly, a less movable cue is more stable than a more movable cue. The movability of a cue may partial be determined by the size of the cue. For example, a small item is easier to move than a large item. The movability of a cue may also be determined by how it is connected to other cues. For example, an isolated item can easily be moved, whereas an item that is attached to a wall is more difficult to move. When the navigators noticed two cues are in conflict, they would rely more on the more stable cue than the less stable cue.

# 4.2.3 2D patterns and isolated objects interact differently with room geometry

In previous studies, wall features and isolated objects were the most widely used cues to contrast the room geometry. As defined by Lee and Spelke (2010a), 2D patterns and isolated objects are both featural cues. This taxonomy is supported by findings that they are both less dominant than room shape during reorientation. Also, Lee and Spelke (2010b) found direct evidence that 2D markings on the wall and isolated objects were not used by children, whereas extended surfaces of similar size and contrast were used by children. However, in Chapter 3 we found that the interaction between room shape and isolated objects and the interaction between room shape and wall features showed different patterns.

Room size has different effects on the relative use of room shape and isolated objects and on the relative use of room shape and wall colors or 2D patterns on the wall (Ratliff & Newcombe, 2008; Sovrano & Vallortigara, 2006; Sovrano, Bisazzaa, & Vallortigara, 2007). As we discussed in the previous section, those effects were attributed to cue stability during retrieval. In Experiment 1 of Chapter 3, on one hand, the isolated objects were more distal in the large room than in the small room, which might suggest the stability of the isolated objects increased in the larger room. One the other hand, the isolated objects should be comparably movable in the small and large rooms because their size was the same regardless of the room size. Meanwhile the movability of the room shape should decrease as room size increased because the large room should be less moveable than the small room. As a result, the relative movability of the room shape decreased with room size, which might suggest the stability of the isolated objects decreased in the larger room. Since the movability of the room was remarkably greater than that of the isolated objects, the effect of movability overwhelmed the effect of feature distance on the relative stability of cues. Therefore, the relative stability of the isolated objects decreased and thus the relative use of the isolated objects decreased as the room was larger.

However, in Experiment 3 of Chapter 3, the wall features (or the walls having those features) and the room were scaled with the same ratio. Therefore, the relative movability of the room and the wall features should not be affected by room size. In this case, the relative stability of the cues was only affected by the distance of the wall features. Since the wall features were more distal in the large room than in the small room, their relative stability with respect to the room shape increased in the larger room. Therefore, the relative use of

the wall features increased in the larger room. In summary, Chapter 3 shows that the properties of isolated objects and wall features are different that could affect their interaction with room geometry. Therefore, it is necessary to consider whether to use isolated objects or wall features as featural cues in future reorientation studies.

#### 4.2.4 Implications and future directions

In daily life, people use various cues to navigate. These cues include inertial cues such as kinetic and vestibular cues, and external cues such as optic flow, landmarks and environment layouts. On one hand, using multiple cues is often advantageous because it increases the accuracy of navigation. For example, a single landmark is sometimes ambiguous, and path integration is erroneous. When both cues are available, navigators may combine the two cues so that they could use path integration to disambiguate the landmark and use the landmark to correct the accumulating errors in path integration. On the other hand, attending to multiple cues may significantly increase cognitive load. And more critically, there may be a problem if the cues conflict each other. Therefore, understanding how cues interact, i.e. how they compete for cognitive resources and weights, is important for understanding navigational behaviors.

In this dissertation, my colleagues and I found that both the properties of the cues and the experience of the navigators may affect cue interaction. Overall speaking, when the participants encounter a novel environment, their encoding of one cue was impaired by encoding another cue. And if the cues conflicted, the participants assigned cue weights based on how well they learned the cues. When the participants gained more experience in the same environment, they became familiar with the environment and learned the relationship between the cues. With this representation of the relationships, encoding one cue was not significantly impaired by

encoding another cue. And if the cues conflicted, the participants assigned cue weights based on the stability of the cues.

Familiarity has been shown to have effects on many navigational behaviors. While it is well established that people who are familiar with an environment usually perform better at place recognition and wayfinding than those who are unfamiliar with the environment (Gollege, 1992), the effect of familiarity on cue interaction is rarely examined. We explained that familiarity affects cue interaction by allowing the navigators to learn the relationship among the cues. Previous studies on the development of spatial knowledge support the idea that people learn the relationship among landmarks and form a cognitive map only after they have gained a certain amount of experience in the environment (Siegel & White, 1975). However, Ishikawa and Montello (2006) argued that the relationship among landmarks are not necessarily learned through time. They found that there were individual differences in the requisition of relationships among landmarks. While some participants learned this knowledge continuously as became familiar with the environment, most participants either learned the relationship from the beginning or never learned the relationship even after repeated exposures. In our studies, we only manipulated whether participants learned the same environment or different environment across trials. We did not directly examine their knowledge about the relationship between the cues. Therefore, further studies are needed to investigate how familiarity affects cue interaction.

Aside from navigators' experience, properties of cues also modulate cue interaction. Previous studies have shown that human adults may be able to optimally combine cues based on cue reliability (e.g., Nardini et al., 2008; Zhao & Warren, 2015b; Chen et al., 2017), where participants assigned more weight to the cue that allowed them to perform more accurately in the spatial task. However, navigators may not always prefer the more accurate cue (Yerramsetti, Marchette, & Shelton, 2013). In our studies, we found that, in familiar environments, cue weighting was affected by a retrieval factor that is independent of the learning accuracy of the cue. We speculate that this retrieval factor may be the stability of the cues. In an adaptive combination theory, Newcombe and Huttenlocher (2006; see also Newcombe & Ratliff, 2007) proposed that multiple cues are combined in a Bayesian fashion with the weight of each cue determined by various properties of the cue, such as reliability, stability, validity and so on. So far, the role of cue reliability in cue combination has been carefully examined, but the roles of other cue properties still need to be investigated.

Moreover, we found that there were huge individual differences in cue preference. For example, in Chapter 3, when the room shape and the features were in conflict, some participants fully relied on the room shape while some fully relied on the features. This preference seems not related to their accuracy of using each cue. And it is very unlikely that those participants who preferred the features believed the features were more stable than the room. In this dissertation, we were unable to further investigate individual differences due to limited sample size and observations for each participant. Future studies are needed to examine what makes people prefer one cue over another cue, how this preference is related to gender, navigational ability and short-term and long-term experience, and whether people which a strong preference could shift to the unfavored cue with minimal effort if they were instructed to.

- Chen, X., McNamara, T. P., Kelly, J. W., & Wolbers, T. (2017). Cue combination in human spatial navigation. *Cognitive Psychology*, *95*, 105–144.
- Cheng, K. (1986). A purely geometric module in the rat's spatial representation. *Cognition,* 23(2), 149-178.
- Cheng, K. (1994). The determination of direction in landmark-based spatial search in pigeons: A further test of the vector sum model. *Animal Learning & Behavior*, 22(3), 291-301.
- Cheng, K. (1995). Landmark-based spatial memory in the pigeon. In D. L. Medin (Ed.), *The psychology of learning and motivation: Advances in research and theory*, Vol. 33, pp. 1-21). San Diego, CA, US: Academic Press.
- Cheng, K., Shettleworth, S. J., Huttenlocher, J., & Rieser, J. J. (2007). Bayesian integration of spatial information. *Psychological Bulletin*, *133*(4), 625.
- Etienne, A. S., Teroni, E., Hurni, C., & Portenier, V. (1990). The effect of a single light cue on homing behaviour of the golden hamster. *Animal Behaviour*, *39*(1), 17-41.
- Foo, P., Warren, W. H., Duchon, A., & Tarr, M. J. (2005). Do humans integrate routes into a cognitive map? Map-versus landmark-based navigation of novel shortcuts. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 31*(2), 195-215.
- Golledge, R. G. (1992). Place recognition and wayfinding: Making sense of space. *Geoforum,* 23(2), 199-214.

- Ishikawa, T., & Montello, D. R. (2006). Spatial knowledge acquisition from direct experience in the environment: Individual differences in the development of metric knowledge and the integration of separately learned places. *Cognitive Psychology*, *52*(2), 93-129.
- Lee, S. A., & Spelke, E. S. (2010a). Two systems of spatial representation underlying navigation. *Experimental Brain Research*, 206(2), 179-188.
- Lee, S. A., & Spelke, E. S. (2010b). A modular geometric mechanism for reorientation in children. *Cognitive Psychology*, *61*(2), 152-176.
- Nardini, M., Jones, P., Bedford, R., & Braddick, O. (2008). Development of cue integration in human navigation. *Current Biology*, *18*(9), 689-693.
- Ratliff, K. R., & Newcombe, N. S. (2008). Reorienting when cues conflict: Evidence for an adaptive-combination view. *Psychological Science*, *19*(12), 1301-1307.
- Shettleworth, S. J., & Sutton, J. E. (2005). Multiple systems for spatial learning: dead reckoning and beacon homing in rats. *Journal of Experimental Psychology: Animal Behavior Processes*, 31(2), 125.
- Siegel, A. W., & White, S. H. (1975). The development of spatial representations of largescale environments. In *Advances in child development and behavior* (Vol. 10, pp. 9-55). JAI.
- Sovrano, V. A., Bisazza, A., & Vallortigara, G. (2005). Animals' use of landmarks and metric information to reorient: Effects of the size of the experimental space. *Cognition*, 97(2), 121–133.
- Sovrano, V. A., Bisazza, A., & Vallortigara, G. (2007). How fish do geometry in large and in small spaces. *Animal Cognition*, *10*, 47–54.

- Sovrano, V. A., & Vallortigara, G. (2006). Dissecting the geometric module. *Psychological Science*, *17*(7), 616-621.
- Yerramsetti, A., Marchette, S. a, & Shelton, A. L. (2013). Accessibility versus accuracy in retrieving spatial memory: evidence for suboptimal assumed headings. *Journal of Experimental Psychology. Learning, Memory, and Cognition, 39*(4), 1106–14.
- Yoganarasimha, D., Yu, X., & Knierim, J. J. (2006). Head direction cell representations maintain internal coherence during conflicting proximal and distal cue rotations:
   Comparison with hippocampal place cells. *Journal of Neuroscience*, *26*(2), 622–631.
- Zhao, M., & Warren, W. H. (2015a). Environmental stability modulates the role of path integration in human navigation. *Cognition*, *142*, 96–109.
- Zhao, M., & Warren, W. H. (2015b). How you get there from here: Interaction of visual landmarks and path integration in human navigation. *Psychological Science*, 26(6), 915-924.

#### Bibliography

- Ashby, F. G., & Townsend, J. T. (1986). Varieties of perceptual independence. *Psychological Review*, 93(2), 154–179.
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014). *Ime4: Linear mixed-effects models using Eigen and S4*. R package version 1.1-7, http://CRAN.R-project.org/package=lme4.
- Bayes, T. (1763). An essay towards solving a problem in the doctrine of chances. *Philosophical Transactions*, *53*, 370-418.
- 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.
- Brown, A. A., Spetch, M. L., & Hurd, P. L. (2007). Growing in circles rearing environment alters spatial navigation in fish. *Psychological Science*, *18*(7), 569-573.
- Buckley, M. G., Smith, A. D., & Haselgrove, M. (2016). Thinking outside of the box:
  Transfer of shape-based reorientation across the boundary of an arena. *Cognitive Psychology*, 87, 53–87.
- Chen, X., & McNamara, T. P. (2014). Bayesian cue interaction in human spatial navigation. In C. Freksa, B. Nebel, M. Hegarty, & T. Barkowsky (Eds.), *Spatial cognition IX* (pp. 147-160). Springer International Publishing.
- Chen, X., McNamara, T. P., Kelly, J. W., & Wolbers, T. (2017). Cue combination in human spatial navigation. *Cognitive Psychology*, 95, 105–144.
- Cheng, K. (1986). A purely geometric module in the rat's spatial representation. *Cognition,* 23(2), 149-178.

- Cheng, K. (1994). The determination of direction in landmark-based spatial search in pigeons: A further test of the vector sum model. *Animal Learning & Behavior*, 22(3), 291-301.
- Cheng, K. (1995). Landmark-based spatial memory in the pigeon. In D. L. Medin (Ed.), *The psychology of learning and motivation: Advances in research and theory*, Vol. 33, pp. 1-21). San Diego, CA, US: Academic Press.
- Cheng, K. (2008). Whither geometry? Troubles of the geometric module. *Trends in Cognitive Sciences*, *12*, 355–361.
- 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 & Review*, 20(6), 1033-1054.
- Cheng, K., & Newcombe, N. S. (2005). Is there a geometric module for spatial orientation? Squaring theory and evidence. *Psychonomic Bulletin & Review*, *12*, 1–23.
- Cheng, K., Shettleworth, S. J., Huttenlocher, J., & Rieser, J. J. (2007). Bayesian integration of spatial information. *Psychological Bulletin*, *133*(4), 625–637.
- Chiandetti, C., Regolin, L., Sovrano, V., & Vallortigara, G. (2007). Spatial reorientation: The effects of space size on the encoding of landmark and geometry information. *Animal Cognition, 10,* 159–168.
- Chiandetti, C., Spelke, E. S., & Vallortigara, G. (2015). Inexperienced newborn chicks use geometry to spontaneously reorient to an artificial social partner. *Developmental Science*, 18(6), 972–978.

- Chiandetti, C., & Vallortigara, G. (2008). Is there an innate geometric module? Effects of experience with angular geometric cues on spatial re-orientation based on the shape of the environment. *Animal Cognition*, *11*(1), 139–146.
- Chiandetti, C., & Vallortigara, G. (2010). Experience and geometry: Controlled-rearing studies with chicks. *Animal Cognition*, *13*(3), 463–470.
- 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*, 105(15), 5915-5920.
- Du, Y., Mahdi, N., Paul, B., & Spetch, M. L. (2016). Cue salience influences the use of height cues in reorientation in pigeons (Columba livia). *Journal of Experimental Psychology: Animal Learning and Cognition*, 42(3), 273–280.
- Du, Y., Spetch, M. L., & Mou, W. (2016). Look up: Human adults use vertical height cues in reorientation. *Memory & Cognition*, 44, 1277-1287.
- Etienne, A. S., & Jeffery, K. J. (2004). Path integration in mammals. *Hippocampus, 14*(2), 180-192.
- Fodor, J. A. (1983). The modularity of mind: An essay on faculty psychology. MIT press.
- Foo, P., Warren, W. H., Duchon, A., & Tarr, M. J. (2005). Do humans integrate routes into a cognitive map? Map- versus landmark-based navigation of novel shortcuts. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 31(2), 195–215.

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

- Golledge, R. G. (1992). Place recognition and wayfinding: Making sense of space. *Geoforum*, 23(2), 199-214.
- 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.
- Gouteux, S., Vauclair, J., & Thinus-Blanc, C. (2001). Reorientation in a small-scale
  environment by 3-, 4-, and 5-year-old children. *Cognitive Development*, 16(3), 853-869.
- Gouteux, S., & Spelke, E. S. (2001). Children's use of geometry and landmarks to reorient in an open space. *Cognition*, *81*(2), 119-148.
- 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*, 44–59.
- Gray, E. R., Bloomfield, L. L., Ferrey, A., Spetch, M. L., & Sturdy, C. B. (2005). Spatial encoding in mountain chickadees: Features overshadow geometry. *Biology Letters*, 1, 314–317.
- 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*, 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. *The Quarterly Journal of Experimental Psychology: Section B*, *56*(1), 114-126.

- Hermer, L., & Spelke, E. S. (1994). A geometric process for spatial reorientation in young children. *Nature*, *370*, 57–59.
- Hermer, L., & Spelke, E. (1996). Modularity and development: The case of spatial reorientation. *Cognition*, *61*, 195–232.
- 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., & Kastsnelson, A. S. (1999). Sources of flexibility in human cognition: Dual-task studies of space and language. *Cognitive Psychology*, 39(1), 3-36.
- Heth, C. D., Cornell, E. H., & Alberts, D. M. (1997). Differential use of landmarks by 8- and 12-year-old children during route reversal navigation. *Journal of Environmental Psychology*, 17(3), 199–213.
- Holden, M. P., Newcombe, N. S., & Shipley, T. F. (2013). Location memory in the real world: Category adjustment effects in 3-dimensional space. *Cognition*, *128*(1), 45-55.
- Hu, Q., Zhang, J., Wu, D., & Shao, Y. (2015). Is height a core geometric cue for navigation?
  Young children's use of height in reorientation. *Journal of Experimental Child Psychology*, 130, 123–131.
- Hupbach, A., & Nadel, L. (2005). Reorientation in a rhombic environment: No evidence for an encapsulated geometric module. *Cognitive Development, 20*(2), 279-302.

- Huttenlocher, J., Hedges, L. V., & Duncan, S. (1991). Categories and particulars: Prototype effects in establishing spatial location. *Psychological Review*, *98*, 352–376.
- Huttenlocher, J., & Lourenco, S. F. (2007). Coding location in enclosed spaces: Is geometry the principle? Developmental Science, 10(6), 741–746.
- Ishikawa, T., & Montello, D. R. (2006). Spatial knowledge acquisition from direct experience in the environment: Individual differences in the development of metric knowledge and the integration of separately learned places. *Cognitive Psychology*, *52*(2), 93-129.
- Kamin, L. J. (1969). Predictability, surprise, attention and conditioning. In B. A. Campbell &
  R. M. Church (Eds.), *Punishment and aversive behavior*, (pp. 276–296). New York:
  Appleton-Century-Crofts.
- Kelly, D. M., Chiandetti, C., & Vallortigara, G. (2011). Re-orienting in space: Do animals use global or local geometry strategies? *Biology Letters*, 7,372–375.
- Kelly, J. W., McNamara, T. P., Bodenheimer, B., Carr, T. H., & Rieser, J. J. (2008). The shape of human navigation: How environmental geometry is used in maintenance of spatial orientation. *Cognition*, 109(2), 281-286.
- Lambinet, V., Wilzeck, C., & Kelly, D. M. (2014). Size does not matter, but features do: Clark's nutcrackers (Nucifraga columbiana) weigh features more heavily than geometry in large and small enclosures. *Behavioural Processes*, 102, 3-11.
- 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, 414–426.
- Lee, S. A., & Spelke, E. S. (2010a). Two systems of spatial representation underlying navigation. *Experimental Brain Research*, 206(2), 179-188.
- Lee, S. A., & Spelke, E. S. (2010b). A modular geometric mechanism for reorientation in children. *Cognitive Psychology*, *61*(2), 152-176.
- Lee, S. A., & Spelke, E. S. (2011). Young children reorient by computing layout geometry, not by matching images of the environment. *Psychonomic Bulletin & Review*, 18(1), 192–198.
- 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, 144-161.
- Legge, E. L., Wystrach, A., Spetch, M. L., & Cheng, K. (2014). Combining sky and earth: desert ants (Melophorus bagoti) show weighted integration of celestial and terrestrial cues. *Journal of Experimental Biology*, 217(23), 4159-4166.
- Leonard, K., Tian, N., Ivanco, T. L., & Kelly, D. M. (2018). Experience with featural-cue reliability influences featural-and geometric-cue use by mice (Mus musculus). *Journal of Comparative Psychology*, 132(1), 106.

- Lever, C., Burton, S., Jeewajee, A., O'Keefe, J., & Burgess, N. (2009). Boundary vector cells in the subiculum of the hippocampal formation. *Journal of Neuroscience*, 29, 9771– 9777.
- Lew, A. R. (2011). Looking Beyond the Boundaries: Time to Put Landmarks Back on the Cognitive Map? *Psychological Bulletin, 137,* 484-507.
- Lubyk, D. M., Dupuis, B., Gutiérrez, L., & Spetch, M. L. (2012). Geometric orientation by humans: angles weigh in. *Psychonomic Bulletin & Review*, *19*(3), 436-442.
- Luce, R. D. (1963). Detection and recognition. In R. D. Luce, R. R. Bush, & E. Galanter (Eds.), *Handbook of mathematical psychology*: Vol. 1 (pp. 103–189). New York: Wiley.
- Maes, J. H., Fontanari, L., & Regolin, L. (2009). Spatial reorientation in rats (Rattus norvegicus): use of geometric and featural information as a function of arena size and feature location. *Behavioural Brain Research*, 201(2), 285-291.
- McClelland, J. L. (1991). Stochastic interactive processes and the effect of context on perception. *Cognitive Psychology*, *23*(1), 1-44.
- Miller, N. Y. (2009). Modeling the effects of enclosure size on geometry learning. Behavioural Processes, 80, 306–313.
- Miller, N. Y., & Shettleworth, S. J. (2007). An associative model of geometry learning. Journal of Experimental Psychology: Animal Behavior Processes, 33, 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*, 419–422.

- Montello, D. R. (1993). Scale and multiple psychologies of space. In *Spatial information theory a theoretical basis for GIS* (pp. 312-321). Springer Berlin Heidelberg.
- Morton, J. (1969). Interaction of information in word recognition. *Psychological Review*, 76(2), 165–178.
- Mou, W., Nankoo J., Zhou, R., & Spetch, M. L. (2014). Use of geometric properties for reorientation to remote cities and local objects. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 40,* 476-491
- Mou, W., & Spetch, M.L. (2013) Object location memory: Integration and competition between multiple context objects but not between observers' body and context objects. *Cognition*, 126(2), 181-197.
- Mou, W., & Zhou, R. (2013). Defining a boundary in goal localization: Infinite number of points or extended surfaces. *Journal of Experimental Psychology: Learning, Memory,* and Cognition, 39(4), 1115.
- Nadel, L., & Hupbach, A. (2006). Cross-species comparisons in development: the case of the spatial 'module'. *Attention and performance XXI*, 499-511.
- 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.
- 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., & Huttenlocher, J. (2006). Development of spatial cognition. In D. Kuhn & R. S. Siegler (Eds.), *Handbook of child psychology: Cognition, perception, and language*, vol. 2 (6th ed., pp. 734–776). New York: Wiley.
- Newcombe, N. S., & Ratliff, K. R. (2007). Explaining the development of spatial reorientation: Modularity-plus-language versus the emergence of adaptive combination. In J. M. Plumert & J. P. Spencer (Eds.), *The emerging spatial mind*, (pp. 63–76). New York: Oxford University Press.
- 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.

Pavlov, I. P. (1927). Conditioned reflexes. New York: Dover.

- 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.
- Pearce, J. M., Ward-Robinson, J., Good, M., Fussell, C., & Aydin, A. (2001). Influence of a beacon on the spatial learning based on the shape of the test environment. *Journal of Experimental Psychology: Animal Behavior Processes, 27*, 329–344.
- R Core Team (2015). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.
- 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.
- Sampaio, C., & Wang, R.F. (2009). Category-based errors and the accessibility of unbiased spatial memories: A retrieval model. *Journal of Experimental Psychology: Learning, Memory, & Cognition, 35,* 1331-1337.
- Shettleworth, S. J., & Sutton, J. E. (2005). Multiple systems for spatial learning: dead reckoning and beacon homing in rats. *Journal of Experimental Psychology: Animal Behavior Processes*, 31(2), 125.
- Siegel, A. W., & White, S. H. (1975). The development of spatial representations of largescale environments. In H. W. Reese (Ed.), *Advances in child development and behavior*: Vol. 10 (pp. 9-55). Academic Press.
- 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,* 199–210.
- Sovrano, V. A., Bisazza, A., & Vallortigara, G. (2005). Animals' use of landmarks and metric information to reorient: Effects of the size of the experimental space. *Cognition*, *97*, 121–133.
- Sovrano, V. A., Bisazza, A., & Vallortigara, G. (2007). How fish do geometry in large and in small spaces. *Animal Cognition*, *10*, 47–54.

- Sovrano, V. A., & Vallortigara, G. (2006). Dissecting the geometric module: A sense linkage for metric and landmark information in animals' spatial reorientation. *Psychological Science*, *17*(7), 616-621.
- Sturz, B. R., Brown, M. F., & Kelly, D. M. (2009). Facilitation learning spatial relations among locations by visual cues: Implications for theoretical accounts of spatial learning. *Psychonomic Bulletin & Review*, 16, 306–312.
- 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 & 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, 246–253.
- Sturz, B. R., & Kelly, D. M. (2013). Environment size and the use of feature and geometric cues for reorientation. *Acta Psychologica*, 142(2), 251-258.
- Sturz, B. R., Kelly, D. M., & Brown, M. F. (2010). Facilitation of learning spatial relations among locations by visual cues: Generality across spatial configurations. *Animal Cognition*, 13, 341–349.
- Stürzl, W., & Zeil, J. (2007). Depth, contrast and view-based homing in outdoor scenes. Biological Cybernetics, 96, 519–531.
- Twilley, L. C., & Dixon, P. (2000). Meaning resolution processes for words: A parallel independent model. *Psychonomic Bulletin & Review*, 7(1), 49-82.

- 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.
- Twyman, A. D., Newcombe, N. S., & Gould, T. J. (2009). Of mice (Mus musculus) and toddlers (Homo sapiens): Evidence for species-general spatial reorientation. *Journal* of Comparative Psychology, 123(3), 342–345.
- Twyman, A. D., Newcombe, N. S., & Gould, T. J. (2013). Malleability in the development of spatial reorientation. *Developmental Psychobiology*, 55(3), 243–255.
- Vallortigara, G. (2009). Animals as natural geometers. In L. Tommasi, M. A. Peterson, & L. Nadel (Eds.), *Cognitive biology* (pp. 83–104). Cambridge: MIT Press.
- Vallortigara, G., Feruglio, M., & Sovrano, V. A. (2005). Reorientation by geometric and landmark information in environments of different sizes. *Developmental Science*, 8, 393–401.
- Wagenmakers, E. J. (2007). A practical solution to the pervasive problems of p values. *Psychonomic Bulletin & Review, 14*, 779-804.
- 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. *Learning & Behavior*, 32, 289– 298.
- Waller, D., & Lippa, Y. (2007). Landmarks as beacons and associative cues: Their role in route learning. *Memory & Cognition*, 35(5), 910–924.
- Wang, L., Mou, W., & Sun, X. (2014). Development of landmark knowledge at decision points. *Spatial Cognition & Computation*, *14*(1), 1-17.
- 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*, 1369–1376.
- Xu, Y. Regier, T., & Newcombe, N. S. (2017). An adaptive cue combination model of human spatial reorientation. *Cognition*, *163*, 56-66.
- Yerramsetti, A., Marchette, S. a, & Shelton, A. L. (2013). Accessibility versus accuracy in retrieving spatial memory: evidence for suboptimal assumed headings. *Journal of Experimental Psychology. Learning, Memory, and Cognition, 39*(4), 1106–14.
- Yoganarasimha, D., Yu, X., & Knierim, J. J. (2006). Head direction cell representations maintain internal coherence during conflicting proximal and distal cue rotations:
  Comparison with hippocampal place cells. *Journal of Neuroscience*, *26*(2), 622–631.
- Zeil, J., Hofmann, M. I., & Chahl, J. S. (2003). Catchment areas of panoramic snapshots in outdoor scenes. *Journal of the Optical Society of America*, 20, 450–469.
- Zhao, M., & Warren, W. H. (2015a). How you get there from here: Interaction of visual landmarks and path integration in human navigation. *Psychological Science*, 26(6), 915-924.
- Zhao, M., & Warren, W. H. (2015b). Environmental stability modulates the role of path integration in human navigation. *Cognition*, *142*, 96–109.