
From Scattering Dots to Cognitive Maps:

Contributions of visual features in localization and cognitive mapping

by

Ruojing Zhou

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

Doctor of Philosophy

Department of Psychology

University of Alberta

Abstract

Localizing oneself and other objects in an environment is important in everyday life. Various visual features available in our surroundings can serve as spatial cues to support accurate localization. Encoding individual locations can be achieved by establishing a vector between a target location and a reference point chosen from the environmental features (e.g., the school is one kilometer north of my home). Representations of individual locations can further be integrated to compose a unified representation, which allows inferring novel spatial relations among the locations (i.e., a vector between two points). Such metric representations are referred to as cognitive maps (e.g., Tolman, 1948) and we refer to the integration process as cognitive mapping. Three sets of studies were carried out to investigate the contributions of different types of visual cues, mainly surface-based boundary cues (e.g., walls or river banks) and discrete-object-based landmark cues (e.g., buildings or trees), in encoding individual locations and cognitive mapping of the locations, respectively.

The studies in Chapter 2 demonstrated a more accurate cognitive map of multiple locations derived from learning locations relative to a single landmark than to a circular boundary. The studies in Chapter 3 revealed two factors that impeded cognitive mapping relative to a circular boundary: 1) that the boundary provided multiple reference points for encoding individual locations, leading to a more complex integration process of single-location representations whereas the integration process was relatively easier when the locations were all encoded relative to the single landmark which served as the common reference point; 2) that participants' knowledge of the spatial relations among the chosen reference points from the boundary was limited, leading to less accurate cognitive maps. The results of the studies in Chapter 3 suggest that people might represent a bounded space in a fragmented fashion rather than in a global fashion. Given the inconsistent roles of a boundary in encoding individual locations (the boundary advantage) and in cognitive mapping, the studies in Chapter 4 investigated two potential factors contributing to the relative preference for the boundary cue in goal localization, mainly the perceived stability of an environmental feature and the distinctiveness of the potential reference points provided by the environmental feature. An overshadowing effect of landmark-related learning over boundary-related learning was observed when the perceived relative stability of the landmark array was increased; however the distinctiveness alone was insufficient to increase the cue reliance upon the landmark array. The results challenged the incidental characteristic of boundary-related learning. We postulate that boundary-related learning might also be subject to a reference-point selection process at the initial stage of goal localization, during which the usefulness of various environmental features are evaluated based on the navigation task and more learning resource would be assigned to the more “informative” feature selected as the reference points for encoding locations.

In sum, our work has demonstrated an inferior role of a boundary cue in forming cognitive maps and the susceptibility of the boundary to the cue competition from other environmental features. We propose the segmentation hypothesis and the vector-addition model to conceptualize localization and cognitive mapping relative to a boundary cue.

Preface

This thesis is an original work by Ruojing Zhou. 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 accepted as R. Zhou, and W. Mou, “Superior cognitive mapping through single landmark-related learning than through boundary-related learning”, Journal of Experimental Psychology: Learning, Memory and Cognition, in press. 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.

Acknowledgments

To my advisor, Weimin Mou, I would like to express my sincere gratitude for all your guidance and support through the course of my graduate studies. Your insight and curiosity towards psychology research keep inspiring me. It is your wisdom, patience and devotion to the students that have nurtured me to continuously grow as an individual both inside and outside research. Thank you for being such an awesome advisor!

To my advisory committee members, Jeremy Caplan and Marcia Spetch, I would like to thank you for all your valuable feedback and support along the way.

To all my labmates in the Virtual Reality and Spatial Cognition Lab, Lei Zhang, Karen Du, Lin Wang and Xuehui Lei, thank you girls for all the intriguing discussions on science and life throughout the years. It is you who have made the lab not only a fascinating place for gaining knowledge but also a big warm family with which life in the lab has always been enjoyable!

To all the former research assistants who helped at different stages of the thesis, Taylor Murphy, Sarah Tan, Auren Poon, Keith Baldoz, So Yon Kwon, Brent Chambers, Benson Ng, Alexandra Vrapciu, Labiqa Nazar, thank you for your time and effort in assisting my work.

To all my dear friends in Edmonton who have poured me with unconditional support during all these years, thank you for all the cheerful jokes, for giving me your shoulders at rough times and for all the adventures you have shared with me. It is you who have made all those otherwise long winters colorful and memorable!

And to my parents, to whom I feel the most grateful, thank you for all your love and trust in me, and for being always there whenever I need. You are the best!

Table of Contents

List of Figures

Chapter 1

General Introduction

Every year between September and October, big flocks of Monarch butterflies fly from Southern Canada/part of the United States to Central Mexico to escape from harsh winters. The cross-continent journey takes the butterflies over two months to finish. The vast plains of Africa witness the largest mammal migration during which hundreds and thousands of wildebeest take a nearly-two-month journey moving from Tanzania to Kenya. These large-scale migrations demonstrate some impressive navigation abilities. Although we humans, compared to our fellow inhabitants on earth, are less competitive regarding our ability to deal with such long-distance, self-initiated navigation, we do need to find our way in our surroundings to various places on a daily basis. To think about how we acquire knowledge of where things are in the environment, how we form memories of various locations in the physical space and eventually use such "mental map" to guide our navigation is fascinating. The quest to understanding the success of a variety of navigation triumphs, from the great migration on a large scale to our seemingly effortless home-to-work commute, would allow us a glimpse of how the mind forms, interacts with and utilizes representations of physical space.

1.1 Place learning and response learning in navigation

Successful navigation relies on accurate encodings and representations of task-relevant spatial information. Spatial information can be acquired in various approaches. One can use proprioceptive and sensorimotor information generated through the course of locomotion to update knowledge regarding one's current location within the environment as well as spatial relations between oneself and the other entities in the environment (Philbeck & Sargent, 2013). Visual features of the environment can also inform an individual regarding one's current location. The current thesis mainly focuses on how the visual features of our surroundings are involved in one’s acquisition of spatial knowledge and forming spatial representation of a given environment.

Multiple learning mechanisms and memory systems can contribute to learning of spatial information of an environment. In his seminal paper, Tolman (1948) distinguished two kinds of learning mechanisms that can lead to a spatial behavior (such as rats running towards a goal location in a maze), namely response learning and place learning. Response learning, as advocated by classic behaviorists, is a type of conditioning during which a certain response is associated with a given stimulus (response can be either strengthened by the presence of a positive stimulus/reward such as food or weakened by the presence of an aversive stimulus/punishment such as an electric shock in animal studies). For instance, when rats are learning to approach a food reward located at the end of the right arm of a T maze placed in the middle of an experiment room, one type of information they can learn is “turning right at the joint leads to food”. Alternatively, rats could also encode the location of the food reward in terms of the environment (e.g., the food is on the west side of the room) and use such location information to guide its behavior in the maze. Tolman referred to the latter as place learning (in which the “place” of an event rather than the action leading to the event was learned)

According to Tolman, place learning is a form of learning fundamentally different from associative learning which includes response learning (Tolman, 1948; see also Nadel, 2013). Through a series of experiments, Tolman and colleagues demonstrated that, among all the results, that 1) rats could use “place” information to reach a goal location containing food reward, in that rats were able to take an alternative path to the goal location when the original trained path was blocked (Tolman, Ritchie & Kalish, 1946); 2) place learning was relatively easier than response learning, in that the learning curve for approaching a specific location for food was steeper than the learning curve for making a consistent action (e.g., turning right at the joint of a T maze) for food in rats (Tolman, Ritchie & Kalish, 1946); 3) the occurrence of place learning was independent of external rewards such as food and immune to the rules of associative learning (Tolman & Honzik, 1930; see also Tolman, 1948). It is through place learning, proposed by Tolman, that rats could build up a comprehensive representation of the environment which stores the metric spatial relations (including distance and direction information) among the environmental features and locations of interest. Tolman termed this type of spatial representation of a given environment as a “cognitive map”, the notion of which stirred a first wave against the then-dominant view of behaviorism account on animal behaviors (which mostly regards animal behavior as a simple mapping between environmental stimuli and responses).

One important property of place learning is that place learning is not subject to competition of associative strength (thus, a form of latent learning), which distinguishes it from associative learning (O’Keefe, & Nadel, 1978). According to the traditional views about associative learning (Rescorla & Wagner, 1972), various environmental stimuli compete for associative strength when an organism is learning to associate a particular stimulus with a specific consequence. As a result, interference such as overshadowing and blocking can be observed in learning the associations between different stimuli and a particular event. Overshadowing refers to the scenario that learning of a more salient stimulus would impair learning of a less salient one when the two stimuli can simultaneously predict an event (Kamin, 1968). Blocking refers to the scenario that initial learning of one stimulus predicting an event interferes (blocks) subsequent learning of the association between a new stimulus and the same event, if the previous stimulus can fully predict the event (Kamin, 1968). As discussed in more detail in the later part of the chapter, the immunity of place learning to overshadowing and blocking (hence, immunity of place learning to competition of associative strength) provides a diagnostic method for researchers to identify a particular navigation behavior/strategy as a form of place learning or associative learning (e.g., Doeller & Burgess, 2008).

Since the original introduction of place learning by Tolman, much research has been done across species to investigate the learning mechanisms involved in goal-oriented navigation behaviors. Various spatial tasks have been developed to assess the acquisition of spatial or non-spatial knowledge in animals and humans. One classic paradigm, the Morris Water Maze (MWM) task is reviewed here because the modification of the task is employed as the main method in the work of this thesis. The Morris Water Maze (MWM) task is one of the prevalent spatial tasks used in animal navigation studies, which has also been adapted for studies on human adults (e.g., Doeller & Burgess, 2008; Mou & Zhou, 2013) and children (e.g., Bullens et al., 2010). The typical setting of the paradigm is that rats are trained to swim to a platform either visible or invisible (submerged) in a tank of opaque water (the shape of the tank can be circular, rectangular or of other forms depending on researchers' interests). The desire to escape from the water would serve as a strong motivation for rats to find the platform. One critical advantage of the MWM task is, depending on the visual cues available during the experiment (either the visible platform itself served as a beacon cue, a visual intramaze landmark, the edge of the tank itself, or the distal visual cues within the room where the tank is located), it is possible to dissociate the roles of various environmental inputs in aiding rats to locate the platform, thus providing a window into understanding the contributions of different learning mechanisms in navigation.

For instance, Morris (1981) demonstrated that rats were able to use both a beaconing strategy (by approaching a visible platform at a fixed location in the tank) and a place learning strategy (by learning the location of a hidden platform at a fixed location in the tank) to locate a platform within the water tank. In this study, two groups of rats were trained to swim to a platform within a circular water tank. The water tank was placed in a room which provided distal visual cues for orientation. For one group (the "cue + place" group), the platform rose from the water surface at a fixed location within the tank, rendering a visible platform meanwhile the platform at the fixed location was submerged for the other group ("place" group). Both groups showed rapid acquisition of the task although the "cue + Place" group displayed faster learning (in terms of steeper decrease in escape latency). Interestingly, when the platform was removed (thus the beacon cue was no longer available for the "cue + place" group), rats in the "cue + place" group still spent more time searching in the correct quadrant than in the other parts of the pool, indicating acquisition of some place knowledge in the cue-place group despite the visibility of the platform as a strong associative cue.

The MWM task not only has advantages in behaviorally disentangling different learning mechanisms underlying a goal-oriented behavior (Brandeis, Brandys & Yehuda, 1989), but also provides a possible means to observe dissociations of different brain systems involved in corresponding learning mechanisms (e.g., Morris, 1982; Packard & McGaugh, 1992; McDonald & White, 1994; Pearce, Roberts & Good, 1998). In general, the findings indicate that distinctive brain areas are involved in different learning mechanisms: notably, the hippocampal region seems to be responsible for place strategies whereas the striatal region seems to be responsible for response strategy when rats are navigating in the maze (for review, see Brandeis, Brandys & Yehuda, 1989; see also White & McDonald 2002).

For example, McDonald and White (1994) trained three groups of rats (hippocampal-lesioned group, dorsal-striatal-lesioned group, and the normal control group) to swim to a visible platform at a fixed location within a circular water tank. Distal orientation cues were available in the room where the tank was located. After every three days of training, the visible platform was replaced with an invisible one occupying the same location to assess rats' ability to locate the platform based on the place strategy (learning the physical location of the platform regardless of the visibility). It was found that the hippocampal-lesioned rats were not able to find the invisible platform still placed at the trained location. In contrast, the dorsal-striatal-lesioned rats were able to locate the platform just as the control rats were. On the last day of the experiment, the researchers moved the visible platform to a new location within the tank to assess rats' ability to locate the platform using the beaconing strategy (visibility as an associative cue). Interestingly, the striatal-lesioned rats still swam to the old location of the platform (trained location) even though the platform was visible at the new location, indicating that the navigation behavior of these rats were controlled by a place strategy. However the hippocampal-lesioned group was able to swim directly to the new location while rats in the control group were split into adopting either a response strategy or a place strategy.

The dissociation between the hippocampal-dependent navigation strategy and the striatal-dependent navigation strategy demonstrates that different brain areas govern place learning and response learning respectively. More critically, these different learning systems seem to process different aspects of environmental information (visibility of the platform as a form of local cue vs. the spatial relation between the platform and the experiment environment as a form of distal cue) in a parallel fashion. Depending on individuals, these parallel learning mechanisms exert controls to different extent over the final spatial behavior displayed by the individuals (as observed in the control group showing split navigation strategies). Such findings led to a theory postulating that multiple parallel memory systems take control of our learning of different aspects of environmental events (McDonald & White, 2002). Information processing within one system is somewhat independent of the processing within another system. As a result, we are able to form different types of memories of our surroundings.

1.2 Visual cues aiding navigation

Our environment has rich visual input, from the sun in the sky, urban buildings in the cities to massive mountain ranges and rivers in nature. We encounter various visual features during our navigation in the environment and naturally some of them are used to help us determine where we are (position) and where we are facing (heading). Two types of visual features and their functions in spatial navigation are identified by researchers (see Lew, 2011 for review), mainly the boundary cues consisted of continuous surface (such as an external wall of a large building or a mountain range) and the landmark cues based on discrete, stand-alone objects (such as a tower or a tree)

1.2.1 Visual landmarks aiding navigation

Visual landmarks are versatile in terms of their roles in aiding navigation. When a destination itself is marked by some visual feature, a beaconing strategy could be employed. For instance, when a prominent skyscraper (can be seen from afar) is the destination of a traveler new to a city, one can simply navigate by approaching the visual landmark. As is discussed before, this type of learning does not necessarily involve place learning (e.g., it is more like response learning of a visible platform in the MWM task). A visual landmark, once registered in our mental representation of a particular space, can also be used for place recognition, that is landmarks of significant navigation relevance can serve as a retrieval cue to notify us what spatial memories are relevant. For instance, upon seeing the familiar bookstore from exiting an underground subway station, we would be able to recognize which exit we took and in which part of the neighborhood we are currently located.

Brain imaging studies have shown that one brain region, parahippocampal place area (PPA) seems to be responsive to objects that are more useful for navigation (Konkle & Oliva, 2012) and to objects that can evoke a strong sense of the surrounding space (Mullaly & Maguire, 2011; see Epstein & Vass, 2014 for review). In one neuroimaging study using the fMRI technique, Janzen and van Turennout (2004) had participants remember objects placed along a route while the participants watched a video footage of the route in a virtual maze. The placement of the objects was critical as some objects were put at the decision points along the route (e.g., at a turning point of the route) and some were not. Participants were later assessed on their memories of the objects in a recognition task. Although behavioral performance on the recognition task was equivalent for decision-point objects and non-decision-point objects, the PPA showed increased activation for decision-point objects than for non-decision-point objects regardless of whether the objects were identified as remembered or not. The results suggest that objects of navigational significance (i.e., landmarks) are processed in an additional stream apart from the processing of non-landmark objects.

Other research has demonstrated that retrosplenial cortex (RSC) is involved in retrieving location and orientation information (i.e., where one is located in terms of a broad environment) based on the given landmark/scene information (e.g., knowing where one is in terms of a neighborhood when seeing the bookstore at the subway exit). In one fMRI study by Vass and

Epstein (2013), participants viewed pictures taken at several familiar campus locations, which consisted pictures from different facing directions at the same location and pictures from different facing directions at different locations. Their behavioral task was to identify the facing direction of the camera when the image was taken upon viewing each picture, which ensured that participants had to recognize the place depicted in a given image to give a correct response. Using multivoxel pattern analysis (MVPA), Vass and Epstein observed that different views across the same location (different facing directions at the same location) elicited more similar activity pattern in RSC than different views at different locations, suggesting a role of RCS in coding location identity (different views across one location indicating the same location). Such findings regarding the roles of different brain regions in response to visual landmarks and scenes reveal the ability of our brain to extract information of navigational significance from our surroundings.

Beyond serving as a beacon cue or a retrieval cue for place recognition, a visual landmark is also useful in establishing stimulus-response associations in navigation. An organism could couple a series of actions with a series of visual landmarks at corresponding decision points to form a type of route knowledge (e.g., turning left at the post office and turning right next at the restaurant) (Siegel & White, 1978; see also Ishikawa & Montello, 2006). Such route knowledge might not involve encoding/representing metric relations among the landmarks, thus falling into the categories of response learning.

As discussed above, discrete objects as visual landmarks of navigational relevance can aid navigation as a beacon cue, a retrieval cue for place recognition or an associative cue for response involved in navigation. Moreover, a single visual landmark can also serve as a reference point for encoding individual locations (e.g., Pearce, Roberts & Good, 1998; Doeller & Burgess, 2008; Mou & Zhou, 2013) when precise knowledge of a location within the space is required (e.g., animals determining a foraging site in outdoor environments). Encoding and representing metric spatial relations between a chosen reference point (a specific landmark) and a target location (i.e., establishing a vector) is involved in this type of spatial learning. However both lesion studies on rats (Pearce, Roberts & Good, 1998) and neuroimaging studies in humans (Doeller, King & Burgess, 2008) have shown that hippocampus, the commonly-regarded locus of place learning, is not necessary in acquisition of this type of vector knowledge between a target location and a single landmark.

In real-life environments, instead of a single landmark, often we find ourselves surrounded by multiple landmarks (e.g., multiple buildings on campus). A target location can, thus, be specified by different landmarks simultaneously. Whether animals can use multiple landmarks to specify a location was of interest in early spatial learning literature. Evidence for this ability has been provided in many species using a transformational paradigm. One typical setting involves subjects learning a target location in the presence of two or more landmarks and they would be later tested with one or some of the landmarks moved from their original spots (e.g., Spetch et al. 1995, Collett et al., 1986). If subjects are just using one of the landmarks to specify the location, then their searching location would either be independent of the transformation (indicating complete reliance on the unmoved landmarks) or follow the shift of the moved landmarks. The in-between results would suggest an averaging strategy. Furthermore how much subjects' searching locations have shifted away from the learning location would indicate the relative weights they assign to each landmark during encoding. The more dominant landmarks would have a greater influence in determining a target location.

Spetch (1995) demonstrated in a touch screen task carried out on both pigeons and humans that spatial learning relative to a landmark would be reduced with the presence of a closer landmark to the target location. On the other hand, it has been shown that rotating distal cues would lead to rats in a water maze task searching at locations corresponding to the rotation manipulation (e.g., McGauran et al., 2004; for review, see Knierim & Hamilton, 2011). Such results indicate that landmarks further away from a target location have more control over the target locations in terms of direction information. The observation that landmarks with different distances to a target location (which could be regarded as a type of cue salience) differ in their control over the spatial learning suggests that spatial learning relative to landmarks might follow some principles of associative learning (e.g., overshadowing)

When learning a target location relative to multiple landmarks, one can establish multiple bearings or vectors between the location and each of the landmarks individually (Kamil & Cheng, 2001). Alternatively, one may also encode the configuration of multiple landmarks and employ this information when encoding a target location. In this approach, the individual identity of landmarks may not be as prominent as when multiple bearings/vectors are established (although Cheng and Spetch [1998] pointed out that the configural information could also be used to identify landmarks).

The evidence for animals using the configuration of an array of landmarks is inconsistent across species. Pigeons were found to search at locations that kept the correct distance and direction from one landmark when an array of four landmarks in test was expanded (Spetch, Cheng & MacDonald, 1996; Spetch et al., 1997). Humans, on the other hand, were found to locate a target at the center of a square-shaped array after expansion when the original location was in the middle of the array (Spetch, Cheng & MacDonald, 1996). Even stronger evidence that humans can use the configuration to locate a specific target completely void of the identity of individual landmark came from the “scramble” paradigm (Spetch, Cheng & MacDonald, 1996). In this experiment, participants were trained to locate a target using an array of visually distinctive landmarks. During testing the landmarks were scrambled so that a strategy of encoding individual vectors between the target locations and each landmark would lead to conflicts of the target locations. However, participants in this design still searched at the location corresponding to the global shape regardless the swapping of the landmarks. Such configuration information from an array of landmarks can be considered as a type of global geometry. To obtain this form of geometric information subjects are likely to extract shape information from the configuration (e.g. the square shape formed by four landmarks) of the landmark array and this shape representation would be independent of the properties of landmarks.

1.2.2 Surface-based boundaries aiding navigation

Apart from landmarks, another major type of spatial cue that draws attention in both reorientation and localization literature is a boundary, referring to a continuous surface forming fully or partially enclosed space in the environment. Geometric information, such as wall length and enclosure shape information derived from the bounded space is thought to be utilized by animals navigating within the boundary. The classic finding of animals encoding the overall shape for reorientation came from a series of experiments carried out in rats by Cheng (1986). It was observed that rats searched equally at both the correct location and the diagonally equivalent location (rotational error) after disorientation even when there was other feature information to unambiguously identify the target location. The exclusive use of the geometric shape (rotational errors were geometrically equivalent to the original locations in a rectangular enclosure) when rats were disoriented led to the speculation that there should be a “metric frame” wired in rats’ mind that specifically processes the geometric properties of the bounded surfaces and this system should be impenetrable to feature information (such as a landmark).

As later other evidence demonstrated that animals of various species adopted strategies other than solely relying on the geometric properties of enclosure shape, modifications to the original geometric module account and other theories have been proposed as well (e.g., view-matching approach, see Cheung, Sturzl, Zeil & Cheng 2008; modularity theory, see Hermer & Spelke, 1994; adaptive combination theory, see Ratliff & Newcombe, 2008; for review, see Cheng, Huttenlocher & Newcombe, 2013).

It is hypothesized that localization relative to a boundaries/extended surface is fundamentally different from localization relative to a single landmark (Doeller & Burgess, 2008). Behaviorally these two kinds of learning are thought to obey principles from two learning mechanisms. Encoding individual locations with respect to an extended boundary falls in the domain of place learning and the process engages the hippocampal activities. In contrast, encoding individual locations relative to a single landmark is thought to be carried out through associative learning (or the response learning system) and the process seems to involve activities in the striatum (Doeller & Burgess, 2008; Doeller, King & Burgess, 2008).

In one of a series of studies, Doeller and Burgess (2008) employed an elegantly designed cue-competition paradigm and a modified version of the WMW task in a desk-top virtual environment to dissociate the encoding process of individual locations relative to a boundary cue and that relative to a single-landmark cue. As discussed earlier, overshadowing and blocking effects are assumed to be important properties of associative/response learning, but not of place learning. Hence, Doeller and Burgess predicted that overshadowing and blocking should be observed in spatial learning relative to a single landmark, whereas spatial learning task relative to a boundary should be immune to such cue competition. In their overshadowing experiment, participants learned four target locations either with the presence of a single landmark (L), a circular boundary (B) or the combination of the two cues (LB). During the subsequent testing phase, the single cue groups (either L or B) were tested with the original learning cues (L-L, B-B), respectively. The two compound cue groups were tested with one of the cues removed (LB-L referred to the group tested with the landmark and LB-B to the group tested with the boundary alone). The results were consistent with the authors' prediction that participants in LB-L group were less accurate localizing the targets during test compared to those in the L-L group, which indicates impaired learning relative to the landmark when the two cues were available. However such impairment was not observed in the LB-B group. A similar pattern of results was obtained in the blocking experiment where initial learning of locations relative to the boundary blocked the subsequent learning relative to the landmark but not vice versa. The authors hence concluded that environmental boundaries have privileged roles in encoding individual locations.

Mou and Zhou (2013), however, hypothesized that in Doeller and Burgess's (2008) study, in addition to the extended surface, boundaries and landmarks differed in the number of reference points. Boundaries contain infinite reference points, which allow vectors from multiple directions to be established between the boundary and a target location. However, a single landmark may provide only one reference point, and hence, allow for only one vector between the landmark and a target location. The number of reference points may be more important for defining a boundary than the extended surface the boundary provides. To test this hypothesis, Mou and Zhou employed a similar overshadowing paradigm where a circular array of 36 identical landmarks was used as the landmark array instead of a single landmark. The landmark array would thus, be regarded to provide more reference points. There were four conditions: L-L, B-B, LB-L and LB-B. The authors defined an impairment effect as the decrease in localization accuracy during testing of the compound-cue conditions compared to that during the learning phase of the same conditions. If participants relied more on one of the cues to encode target locations during learning, one would expect to see poorer performance during test when the more dominant cue was removed. The results surprisingly showed that participants were not affected by removal of either cue. Hence the authors proposed that a discrete landmark array consisting of multiple reference points (even though it did not contain a continuous surface) might be sufficient to invoke a boundary-like representation.

Studies using single-cell recording techniques have also provided a window looking into how the hippocampus processes boundary information as an input to code “place”. Place cells, discovered in the hippocampus of both rats (O’Keefe & Dostrovsky, 1971; O’Keefe, 1976) and humans (Ekstrom et al., 2003), are shown to display place-specific firing, that is a place cell will reach its peak firing rate when an organism (a rat or a human) are in a specific region within a bounded space (the region is the place field of the particular cell). At least in rats, such firing seems to be controlled by the walls surrounding an enclosure in which rats are moving (O’Keefe & Burgess, 1996). A boundary-vector-cell (BVC) model was proposed to explain how place cells are tuned to respond to the continuous surfaces forming a bounded environment (Hartley et al., 2000, Barry et al. 2006, Barry & Burgess, 2007). Boundary vector cells (BVCs) are hypothesized to fire in response to a barrier (e.g., a piece of boundary or edge) subtending a visual angle from an observer’s location. Different BVCs are thought to tune to different barriers located at their preferred distances and from preferred allocentric directions. The summed firings of subsets of BVCs serve as inputs to a corresponding place cell, whose firing is then responsive to relative locations of barriers around an animal. Both distance information and allocentric direction information are important to the firings of BVCs (Hartley et al., 2000), thus, to the firings of place cells. Later research has identified border cells in rats' entorhinal cortex (Solstad, Boccara, Kropff, Moser & Moser, 2008) and boundary vector cells in the subiculum of rats' hippocampal formation (Lever, Burton, Jeewajee, O'Keefe & Burgess, 2009), providing further evidence for environmental boundaries serving as a critical input in spatial representations formed by the hippocampal system.

1.3 From scattering dots to cognitive maps

When we use our memory of our home city to guide our daily commute, not only do we want to know where each of our destinations is with respect to some reference points (salient environmental features can serve as reference points, such as where the grocery store is in terms of one's home), but most importantly how these isolated destinations are spatially connected with each other. In this sense, the mental map rooted in our mind should be able to integrate knowledge of individual locations acquired from separate navigation experience into a unified representation, which allows inferring spatial relations among the locations (i.e., a vector between two points). Such metric representations are referred to as cognitive maps (e.g., Tolman, 1948) and we refer to the integration process as cognitive mapping. One of the major themes of the current thesis is to investigate the roles of different environmental features (such as boundaries and landmarks) and their corresponding processing streams (e.g., place learning vs.

response learning) in encoding individual locations (thus, the scattering dots on the "map") as well as in forming cognitive maps.

Tolman (1948) emphasized in his proposal that place learning led to a representation of our surroundings in a broad, flexible, map-like fashion which records not only the spatial properties of entities (e.g., locations of the entities) within the space but also the spatial relations among the entities. Therefore, one defining property (or one vital advantage) of such representation is that cognitive maps allow inference of novel spatial relations between two points in the space while direct navigation experience between the two points is not obtained previously (some researchers refer to such ability as taking a "short-cut").

As discussed in the previous section, place learning was hypothesized to contribute to forming cognitive maps. The idea is further developed by O'Keefe and Nadel (1978) in their cognitive map theory, which postulated that the hippocampal formation processes various information through the course of navigation (e.g., visual features of an environment, motor signals from locomotion) to form cognitive maps. Moreover the hippocampus is also responsible for storage of cognitive maps. In accordance with this theory, neuroimaging studies on humans have shown that the human hippocampus is involved in encoding navigation-related information (Maguire, Frackowiak & Frith, 1996), long-term representation of spatial layouts (Maguire, Frackowiak & Frith, 1997). Other studies using a spatial task which could be solved in two different approaches (the place-learning system or the response-learning system) demonstrated that adopting a place-learning strategy activated the hippocampus and allowed flexible navigation such as taking novel short cuts whereas adopting a response-learning strategy activated the striatum (Marchette, Bakker, & Shelton, 2011; Iaria, Petrides, Dagher, Pike, & Bohbot, 2003).

Although hippocampal formation has long been regarded as indispensable in encoding spatial information and in forming cognitive maps, different theories have been proposed regarding the role of hippocampus in the long-term storage of cognitive maps. The multiple trace theory proposed by Nadel and Moscovitch (1997, see also Moscovitch et al., 2005) hypothesized that the hippocampus might be important in constructing detailed or episodic spatial memory, which consists of a rich context, whereas extra-hippocampal structures might be important in semantic spatial memory. Studies on patients who suffered from brain damage provided supporting evidence for the argument. In particular, patients with hippocampal lesion still exhibited some maintenance of long-term spatial knowledge and in some case were even able to form new spatial memories (Corkin, 2002; Bohbot et al., 1998; Teng & Squire, 1999).

1.4 Outline of the Thesis

One of the main research interests of this thesis is to investigate the contributions of different types of visual cues, mainly surface-based boundary cues and discrete-object-based landmark cues in encoding individual locations and cognitive mapping of the locations, respectively. By understanding how the two types of environmental visual features engaged in our acquisition of spatial knowledge during the development of a cognitive map of a given environment, we reflect upon the dichotomous view towards the two learning systems (hippocampal place-learning vs. striatal response-learning) in terms of their contributions in forming spatial memories.

In Chapter 2, we investigate the relative quality of cognitive maps derived from a single landmark cue and from a surface-based boundary cue. As mentioned in the general introduction, boundary advantage has been observed in spatial tasks such as encoding individual locations and learning relative to a boundary cue is thought to engage hippocampal-dependent place learning. In contrast, learning locations relative to a single landmark seems to be processed through striatal-dependent response learning. It is not clear whether such boundary advantage would also benefit cognitive mapping given the importance of place learning and hippocampal-activity in forming cognitive maps. Participants learned four objects' locations either relative to a circular boundary or to a single landmark. Their cognitive mapping knowledge was tested with two spatial tasks that required inference of novel spatial relations among the locations. The results indicate a landmark advantage in forming cognitive maps, that is a more accurate cognitive map of the four locations was derived from the landmark cue than from the boundary cue.

In Chapter 3, recognizing the inferior cognitive maps derived from a surface-based boundary cue, we investigate whether the larger number of reference points provided by a boundary would lead to a worse cognitive map and whether a lack of knowledge about the direct spatial relations among the multiple reference points from a boundary would also lead to worse cognitive mapping. We manipulated the number of reference points available in the environment (from one, four to a boundary containing an infinite number of reference points in Experiment 1) and the degree of availability regarding the knowledge of the direct spatial relations among the reference points (Experiment 2) when participants were learning four locations. The results demonstrated that less accurate cognitive maps were developed when the number of reference points increased. Moreover a lack of knowledge about the spatial relations among chosen reference points impeded cognitive mapping relative to the boundary. Localization process relative to a circular boundary is discussed under the segmentation hypothesis which postulates a global boundary might be segmented into local sections of reference points and only the most informative segments for a particular location are attended to when participants are encoding that location.

In Chapter 4, recognizing the inconsistent findings regarding the boundary advantage in encoding individual locations and the single-landmark advantage in cognitive mapping, we investigate how boundary advantage occurs in representing individual locations. Experiment 1, using both an overshadowing paradigm and a cognitive mapping task, we replicated the findings that participants preferred a circular boundary to a four-landmark array for encoding four locations however the cognitive maps of these locations derived from the landmark array were more accurate. Using the overshadowing paradigm, we manipulated the relative stability and distinctiveness of the two cues in Experiment 2 and 3. The results showed that increasing the stability of the landmark array decreased the overall reliance on the boundary cue in encoding individual locations (overshadowing of the landmark array to the boundary was observed), providing supporting evidence that a boundary cue might also be subject to cue competition. Localization with the presence of multiple visual features is discussed under the reference-point selection hypothesis. We speculate that various environmental features are evaluated in terms of their perceived "usefulness" (cue validity) in completing a specific navigation task and learning resources are assigned accordingly to the environmental features.

In Chapter 5, the results of the studies in the thesis are summarized. Localization processes relative to a homogenous boundary cue (including encoding individual locations and cognitive mapping of multiple locations) are discussed. Furthermore I reflect upon the traditional dichotomous view towards place learning and response learning.

1.5 References

Barry, C., Lever, C., Hayman, R., Hartley, T., Burton, S., O'Keefe, J., Jeffery, H., & Burgess, N. (2006). The boundary vector cell model of place cell firing and spatial memory. *Reviews in the Neurosciences*, *17*(1-2), 71-97.

Barry, C., & Burgess, N. (2007). Learning in a geometric model of place cell firing. *Hippocampus*, *17*(9), 786-800.

Bohbot, V. D., Kaline, M., Stepankova, K., Spackova, N., Petrides, M., & Nadel, L. (1998). Spatial memory deficits in patients with lesions to the right hippocampus and to the right parahippocampal cortex. *Neuropsychologia*, *36*(11), 1217-1238.

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

Brandeis, R., Brandys, Y., & Yehuda, S. (1989). The use of the Morris Water Maze in the study of memory and learning. *International Journal of Neuroscience, 48*, 29-69.

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

Cheng, K., & Spetch, M. L. (1998). Mechanisms of landmark use in mammals and birds. In S. Healy (Ed.). Spatial Representation in Animals, Oxford: Oxford University Press, pp. 1-17.

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*, 1033-1054.

Cheung, A., Sturzl, W., Zeli, J. (2008). The Information Content of Panoramic Images II: View-based navigation in nonrectangular experimental arenas. *Journal of Experimental Psychology: Animal Behavior Processes, 34*(1), 15-30.

Collett, T.S., Cartwrigth, B.A., & Smith, B.A. (1986). Landmark learning and visuo-spatial memories in gerbils. Journal of Comparative Physiology, 158, 835-851.

Corkin, S. (2002). What's new with the amnesic patient H. M.? *Nature Reviews Neuroscience*, *3*, 153-160.

Doeller, C. F., & Burgess, N. (2008). Distinct error-correcting and incidental learning of location relative to landmarks and boundaries. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(15), 5909-5914.

Doeller, C. F., King, J. A., & Burgess, N. (2008). Parallel striatal and hippocampal systems for landmarks and boundaries in spatial memory. *Proceedings of the National Academy of Sciences of the United States of Americ*a, *105*(15), 5915-5920.

Ekstrom, A. D., Kahana, M. J., Caplan, J. B., Fields, T. A., Isham, E. A., Newman, E. L., & Fried, I. (2003). Cellular networks underlying human spatial navigation. *Nature*, *425*, 184-188.

Epstein, R. A., & Vass, L. K. (2014). Neural systems for landmark-based wayfinding in humans. *Philosophical Transactions of the Royal Society Biological Sciences*, *369*(1635), 20120533.

Hartley, T., Burgess, N., Lever, C., Cacucci, F., & O'Keefe, J. (2000). Modeling place fields in terms of the cortical inputs to the hippocampus. *Hippocampus, 10*, 369-379.

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

Iaria, G., Petrides, M., Dagher, A., Pike B., & Bohbot, V. D. (2003). Cognitive strategies dependent on the hippocampus and caudate nucleus in human navigation: Variability and change with practice. *The Journal of Neuroscience*, *23*(13), 5945-5952.

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*, 93-129.

Janzen, G., & van Turennout, M. (2004). Selective neural representation of objects relevant for navigation. *Nature Neuroscience*, *7*, 673–677.

Kamil, A.C., & Cheng, K. (2001). Way-finding and landmarks: the multiple-bearings hypothesis. *Journal of Experimental Biology, 204*, 103-113.

Kamin. L. J. Attention-like processes in classical conditioning. In M. R. Jones (Ed.), Miami Symposium on the prediction of behavior: Aversive stimulation. Miami: Universily of Miami Press, 1968.

Knierim, J., & Hamilton, D. A. (2010). Framing spatial cognition: neural representation of proximal and distal frames of reference and their roles in navigation. *Physiological Reviews, 91*, 1245-1279.

Konkle, T., & Oliva, A. (2012). A real-world size organization of object responses in occipitotemporal cortex. *Neuron*, *74*, 1114–1124.

Lever, C., Burtonm S., Jeewajee, A., O'Keefe, J., & Burgess, N. (2009). Boundary vector cells in the subiculum of the hippocampal formation. *Journal of Neuroscience, 29*(31), 9771-9777.

Lew, A. R. (2011). Looking Beyond the Boundaries: Time to put Landmarks back on the cognitive map? *Psychological Bulletin, 137*(3), 454-507.

Maguire, E. A., Frackowiak, R. S. J., & Frith, C. D. (1996). Learning to find your way: a role for the human hippocampal region. *Proceedings of Royal Society London [Biology], 263*, 1745–1750.

Maguire, E. A., Frackowiak, R. S. J., & Frith, C. D. (1997). Recalling Routes around London: Activation of the Right Hippocampus in Taxi Drivers. *Journal of Neuroscience, 17*(18), 7103-7110.

Marchette, S. A., Bakker, A., & Shelton, A. L. (2011). Cognitive mappers to creatures of habit: Differentail engagement of place and response learning mechanisms predicts human navigational behavior. *The Journal of Neuroscience*, *31*(43), 15264-15268.

McDonald, R. J., & White, N. M. (1994). Parallel information processing in the water maze: evidence for independent memory systems involving dorsal striatum and hippocampus. *Behavioral Neural Biology*, *61*(3), 260-270.

Morris, R. G. M. (1981). Spatial localization does not require the presence of local cues. *Learning and Motivation*, *12*, 239-260.

Morris, R. G. M. (1982). Place navigation impaired in rats with hippocmpal lesions. *Nature*, *297*, 681-683.

Moscovitch, M., Rosenbaum, R. S., Gilboa, A., Addis, D. R., Westmacott, R., Grady, C., McAndrews, M. P., Levine, B., Black, S., Winocur, G., & Nadel, L. (2005). Functional neuroanatomy of remote episodic, semantic and spatial memory: a unified account based on multiple trace theory. *Journal of Anatomy*, *207*, 35-66.

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), 1115-1127.

Mullally, S. L., & Maguire, E. A. (2011). A new role for the parahippocampal cortex in representing space. *Journal of Neuroscience*, *31*, 7441–7449.

MvGauran, A.T., Harvey, D., Cunningham, L., Craig, S., & Commins, S. (2004). Retention of cue-based associations in the water maze is time-dependent and sensitive to disruption by rotating the starting position. *Behavioral brain research, 151*, 255-266.

Nadel, L. (2013). Cognitive maps. In D. Waller & L. Nadel (Eds.), *Handbook of spatial cognition* (pp. 155-171). Washington, DC, US: American Psychological Association.

Nadel, L., & Moscovitch, M. (1997). Memory consolidation, retrograde amnesia and the hippocampal complex. *Current Opinion of Neurobiology*, *7*, 217–227.

O'Keefe, J., & Burgess, N. (1996). Geometric determinants of the place fields of hippocampal neurons. *Nature, 381*, 425-428.

O'Keefe, J., & Dostrovsky, J. (1971). The hippocampus as a spatial map. Preliminary evidence from unit activity in the freely-moving rat. *Brain Research*, *34*, 171-175.

O'Keefe, J. (1976). Place Units in the Hippocampus of the Freely Moving Rat. *Experimental Neurology*, *51*, 78-109.

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

Parkard, M. G., & McGaugh, J. L. (1992). Double dissociation of fornix and caudate nucleus lesions on acquisition of two Water Maze Tasks: Further evidence for multiple memory systems. *Behavioral Neuroscience, 106*(3), 439-446.

Pearce, J. M., Roberts, A. D. L., & Good, M. (1998). Hippocampal lesions disrupt navigation based on cognitive maps but not heading vectors. *Nature*, *396*, 75-77.

Ratliff, K. R., & Newcombe, N. S. (2008). Reorienting when cues conflict: evidence for an adaptive-combination view. *Psychological Science, 19*, 1301-1307.

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

Siegel, A. W., & White, S. H. (1975). The development of spatial representations of large-scale environments. In H. W. Reese (Ed.), *Advances in child development and behavior* (Vol. 10, 9-55). New York: Academic Press.

Spetch, M. L. (1995). Overshadowing in landmark learning: Touch-screen studies with pigeons and humans. *Journal of Experimental Psychology: Animal Behavior Processes, 21*, 166-181.

Spetch, M. L., Cheng, K., & MacDonald, S. E. (1996). Learning the configuration of a landmark array, I: Touch screen studies with pigeons and humans. *Journal of Comparative Psychology, 110*, 55-68.

Spetch, M. L., Cheng, K., MacDonald, S. E., Linkenhoker, B. A., Kelly, D.M., & Doerkson, S. R. (1997). Use of landmark configuration in pigeons and humans: II. Generality across search tasks. *Journal of Comparative Psychology, 111*, 14-24.

Solstad, T., Boccara, C. N., Kropff, E., Moser, M. B., & Moser, E. I. (2008). Representation of geometric borders in the entorhinal cortex. *Science, 322*(5909), 1865-1868.

Teng, E., & Squire, L. R. (1999). Memory for places learned long ago is intact after hippocampal damage. *Nature*, *400*, 675-677.

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

Tolman, E. C., & Honzik, C. H. (1930). "Insight" in rats. University of California, Publications in Psychology, 4, 215-232.

Tolman, E. C., Ritchie, B. F., & Kalish, D. (1946). Studies in spatial learning II: Place learning versus response learning. *Journal of Experimental Psychology*, *36*(3), 221-229.

Vass, L. K. & Epstein, R. A. (2013). Abstract representations of location and facing direction in the human brain. *The Journal of Neuroscience*, *33*(14), 6133-6142.

White, N. M., & McDonald, R. J. (2002). Multiple parallel memory systems in the brain of the rat. *Neurobiology of Learning and Memory*, *77*(2), 125-184.

Chapter 2

Superior Cognitive Mapping through Single-landmark-related Learning than through Boundary-related Learning

A version of this work was previously published as: **Zhou, R.**, & Mou, W. (2016). Superior cognitive mapping through single landmark-related learning than through boundary-related learning. *Journal of Experimental Psychology: Learning, Memory and Cognition,* in press.

2.1 Abstract

Cognitive mapping is assumed to be through hippocampus-dependent place learning rather than striatum-dependent response learning. However, we propose that either type of spatial learning, as long as it involves encoding metric relations between locations and reference points, could lead to a cognitive map; furthermore the fewer reference points to specify individual locations, the more accurate a cognitive map of these locations will be. We then demonstrate that participants have more accurate representations of vectors between two locations and of configurations among three locations when locations are individually encoded in terms of a single landmark than when locations are encoded in terms of a boundary. Previous findings show that learning locations relative to a boundary involves stronger place learning and higher hippocampal activation whereas learning relative to a single landmark involves stronger response learning and higher striatal activation. Recognizing this, we provide evidence challenging the cognitive map theory but favouring our proposal.

2.2 Introduction

Navigation between two locations is a crucial task for everyday life and can rely on two different kinds of spatial knowledge. The first involves representing a sequence of responses (i.e., turns) along a path between locations; the other involves representing metric relationships, (i.e. straight-line distance and direction) among locations (Siegel & White, 1975). Tolman (1948) originally referred to the second type of knowledge, but not the first one, as a cognitive map, analogous to an external map representing metric relationships among places. In the current study, consistent with Tolman (1948) and other researchers (Bennett, 1996; Nadel, 2013; O'Keefe & Nadel, 1978), we consider a cognitive map as a mental representation of metric relations among individual locations. The hallmark functions of a cognitive map are to enable people to infer spatial relations between two locations (Levine, Jankovic, & Palij, 1982; Tolman, 1948), and to judge the spatial configuration among multiple locations (Evans & Pezdek, 1980; Thorndyke & Hayes-Roth, 1982). In the current study, we examine a cognitive map of an environment in terms of these two hallmark functions.

Tolman (1948) attributed the construction of cognitive maps to latent place learning in contrast with response learning through stimulus-response association. Tolman's cognitive map theory was further developed by O'Keefe and Nadel (1978). They proposed that there are two systems involved in spatial learning: the locale system and the taxon system. The locale system, corresponding to place learning, is hypothesized to be a major contribution to cognitive mapping and to rely on the hippocampus. By contrast, the taxon system is assumed to be important in encoding a sequence of responses (e.g. turns along a route), corresponding to stimulus-response association and independent of the hippocampus. In the current paper, we refer to theories claiming that the hippocampus and place learning are critical to cognitive mapping as the cognitive map theory. The cognitive map theory has been supported by many empirical studies (Iaria, Petrides, Dagher, Pike, & Bohot, 2003; Ekstrom, et al., 2003; Hartley, Maguire, Spiers, & Burgess, 2003; Marchette, Bakker, & Shelton, 2011; McDonald & White, 1994; O'Keefe & Dostrovsky, 1971).

However, a growing body of evidence indicates that metric relations among locations might also be learned and stored independent of the hippocampus (Aguirre & D'Esposito, 1997; Bohbot et al., 1998; Corkin, 2002; Maguire, Nannery, & Spiers, 2006; Miller, Vedder, Law, & Smith, 2014; Moscovitch et al., 2005; Pearce, Roberts, & Good, 1998; Teng & Squire, 1999; Vass & Epstein, 2013; Wolbers & Büchel, 2005). For example, Pearce et al. (1998) reported that rats with hippocampal lesions could find the target location that had a fixed metric relation to a movable landmark across trials. Vass and Epstein (2013; see also Epstein & Vass, 2014) proposed that the retrosplenial complex might be important in encoding locations and directions in a large-scale environment.

Furthermore, some studies suggest that metric relations can be acquired through response learning and independent of the hippocampus. Doeller and Burgess (2008) demonstrated that learning locations relative to a single landmark was overshadowed and blocked by learning relative to a continuous boundary. They concluded that spatial learning relative to a landmark involves response learning whereas spatial learning relative to a boundary involves latent place learning. Moreover the same study demonstrated that participants localized objects with equivalent accuracy when learning with either cue alone, indicating that metric relations can be acquired through response learning. In another neuroimaging study (Doeller, King, & Burgess, 2008), the striatum was shown to be involved in encoding and remembering individual locations relative to a landmark, whereas the hippocampus was involved in boundary-related spatial learning, indicating that people encode individual locations relative to a landmark through response learning that is less hippocampal-dependent.

Inspired by these findings, we hypothesize that as long as spatial learning produces the encodings of metric relations from locations to a common reference (e.g. a circular boundary, a landmark), regardless of the extent to which place learning and hippocampus are involved, it contributes to a cognitive map of the locations. Furthermore, we hypothesize that a cognitive map of locations is more accurate when the locations are encoded relative to a single reference point than when the locations are encoded relative to multiple reference points. When there is only one reference point, every location is encoded relative to the same reference point (see Figure 2.1A for illustrations). Suppose there are two locations, a and b, encoded relative to the single reference point, R. People can compute the vectors between any two locations (e.g., $V_{a\text{-}b}$ in Figure 2.1A) by adding the two vectors between each location and the reference point (e.g., $V_{a\text{-}R}$ + $(-V_{b\text{-}R})$). When there are multiple reference points (e.g. R1, R2 in Figure 2.1B), different locations might be encoded relative to different reference points (e.g., $V_{a\text{-}R1}$, $V_{b\text{-}R2}$). When people compute the vectors between two target locations (e.g., $V_{a\text{-}b}$), they have to add not only the two vectors between the individual locations and their corresponding reference points, but also the vector between the two reference points (e.g., $V_{a\text{-}R1} + (-V_{b\text{-}R2}) + V_{R1\text{-}R2}$). Extra errors might be involved in encoding and adding the vectors between different reference points (e.g., $V_{R1\text{-}R2}$), leading to a less accurate cognitive map of vectors between locations. We refer to this hypothesis as the vector addition model.

Two experiments were designed to distinguish this vector addition model from the cognitive map theory. These experiments were based on the findings that compared with single-landmark-relative learning, boundary-related learning involves more place learning and stronger hippocampal activation (e.g., Doeller & Burgess, 2008; Doeller et al., 2008). According to the cognitive map theory, cognitive mapping relies on place learning and the hippocampus. Therefore, boundary-related spatial learning should lead to a better cognitive map of locations. In contrast, according to the vector addition model, people develop a better cognitive map when there is a single reference point than when there are multiple reference points. Because a boundary consists of multiple reference points and a single landmark has one reference point (Mou & Zhou, 2013), spatial learning relative to a single landmark should lead to a better cognitive map.

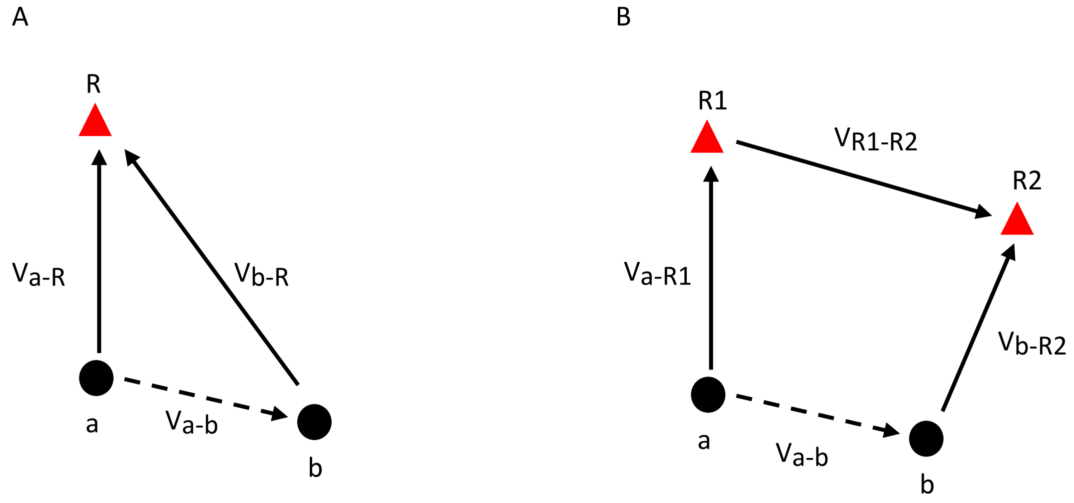


Figure 2.1. Schematic illustrations of the vector addition model. A, inferring the spatial relations between locations a and b when both locations are encoded relative to a single reference point R. The solid lines show the vectors from target locations to the reference point, $V_{a\text{-}R}$ and $V_{b\text{-}R}$. The dashed line shows the inferred vector between the two locations, $V_{a\text{-}b} = V_{a\text{-}R} + (-V_{b\text{-}R})$; B,

inferring the spatial relations between locations a and b when a is encoded relative to the reference point R1 and b relative to R2. The solid lines with arrows show, respectively, the encoded vectors from a to R1 ($V_{a\text{-}R1}$), from R1 to R2 ($V_{R1\text{-}R2}$) and from b to R2 ($V_{b\text{-}R2}$). The dashed line shows the inferred vector between the two locations, $V_{a\text{-}b} = V_{a\text{-}R} + V_{R1\text{-}R2} + (-V_{b\text{-}R})$.

2.3 Experiment 1

Participants learned four objects' locations individually with either a boundary cue or a landmark cue. A task requiring inference of the spatial relation between two objects was employed to evaluate the accuracy of the cognitive map of objects' locations in either learning-cue condition.

2.3.1 Method

Participants. Forty-eight (24 males and 24 females) students from the University of Alberta participated to fulfill a course requirement.

Materials and Design. An immersive virtual environment was displayed using an nVisor SX60 head-mounted display (HMD) (NVIS Inc., Virginia). Graphics were rendered using the Vizard software (WorldViz, Santa Barbara, California). Head orientation was tracked with an InterSense IS-900 motion tracking system (InterSense Inc., Massachusetts). Thus, through head rotation, participants could change their viewpoints. Participants used a joystick to translate, to pick up and to place back the objects in the virtual environment.

In the virtual environment (see Figure 2.2), participants learned four locations on infinite grassland by picking up four sequentially presented objects (a candle, a lock, a bottle and a wood block) and then placing them at the correct locations. Two sets of locations were used (referred to as Configuration 1 and Configuration 2 respectively) and half of the participants learned Configuration 1. The object-location pair was randomized across participants. During the learning phase, either a visually homogeneous, circular wall (the boundary condition, referred to as B, Figure 2.2A) or a visually homogeneous traffic cone (the landmark condition, referred to as L, Figure 2.2B) was presented as the localization cue. Four different scenes (Ocean, Forest, Mountain and City) were set at infinity as distal orientation cues (indicated by the surrounding labels in Figure 2.2). Without distal orientation cues, it is impossible to specify an object's location in terms of the traffic cone or the circular wall. In the testing phase (Figure 2.2C), the landmark in L or the wall in B was removed but one of the four objects was presented in each trial as the localization cue, together with the distal orientation cues. Participants needed to replace the other three objects. Because participants never saw the four objects simultaneously, the vectors between the cue objects and the probed objects must have been a product of cognitive mapping. Therefore, participants' testing performance in L or B could reflect the relative accuracy of cognitive mapping in each condition.

Procedure. Participants donned the HMD and sat on a swivel chair at the center of the experiment room. Each participant went through three phases: the pick-up phase, the learning phase and the testing phase. During the pick-up phase, participants collected the four objects one by one from their original locations (only one object appeared at its correct location for participants to collect each time). The localization cues (the wall in B and the traffic cone in L) as well as the distal orientation cues were presented during the pick-up phase. The learning phase comprised four blocks of four learning trials (one trial per object in each block). For each trial, one of the four objects was probed and participants replaced the probed object using their memory. After the response, the probed object appeared at its original location. Participants were asked to collect it. Participants' starting locations (within 40 virtual meters from the center of the wall) and facing directions at the beginning of each trial were randomized. During testing, the boundary in B and the landmark in L were removed. For each trial, one of the four objects was shown at its original location as a localization cue together with the distal orientation cues; participants replaced one of the other three objects. The testing phase comprised four blocks of three testing trials. In each block, one of the four objects served as the testing cue in all three trials and each of the other three objects was probed once. No feedback was given in the testing phase.

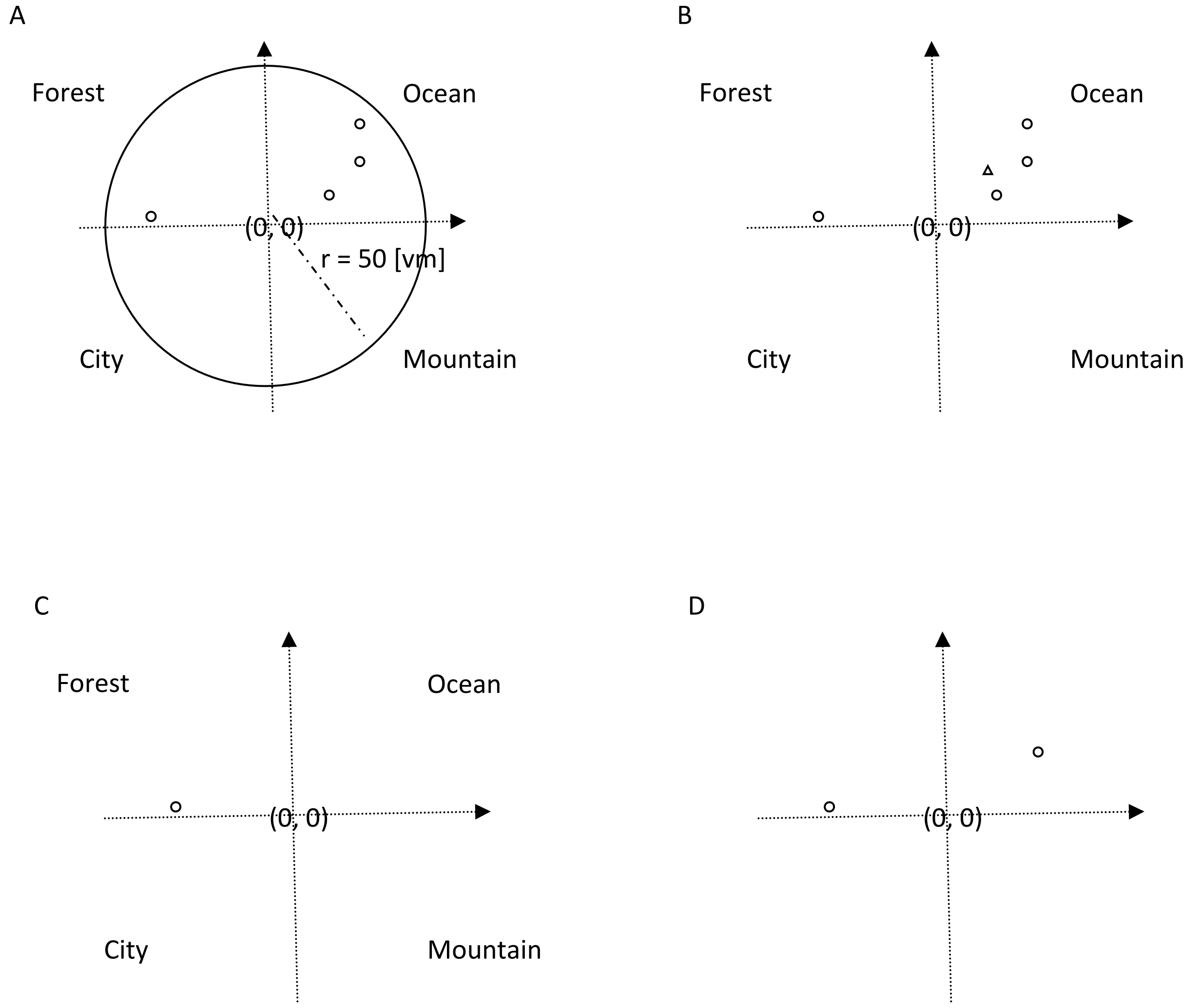


Figure 2.2. Top-view illustrations of the virtual environments used in Experiment 1 and 2. A, The learning phase of the boundary condition in both experiments. The circle illustrates the wall, 50 virtual meters (vms) in radius which is also illustrated as the dashed line in the circle. The two dotted lines with arrows illustrate the coordinate axes where the (0, 0) is the origin of the coordinate system (also the center of the wall) used in the virtual-reality environment. The axes and the center are marked only for readers. The four dots illustrate the target locations from Configuration 1. The coordinates of the four locations in Configuration 1 are (19.94, 9.30),

(29.44, 32.70), (-33.92, 2.37), (29.35, 19.06) respectively; the coordinates of the four target locations in Configuration 2 (not depicted here) are (35.86, 19.88), (-7.74, -31.05), (-5.14, 6.13), (-18.02, -12.62) respectively (units in vms). The four labels (Ocean, Mountain, City, and Forest) illustrate the background scenes set at infinity from the center of the environment; B, The learning phase of the landmark condition in both experiments. The triangle illustrates the traffic cone used as the landmark cue, which was placed at (18, 18); C, The testing phase in Experiment 1. The dot illustrates one of the four objects at its original location used as the testing cue for one particular trial. The original localization cue (the landmark or the boundary) was removed; D, The testing phase in Experiment 2. The two dots illustrate two of the four objects at their original locations used as the testing cues for one particular trial. Both the original localization cue and the original orientation cues (i.e. the background scenes) were removed.

2.3.2 Results and Discussion

Response errors, measured as the distances between participants' response locations and the corresponding correct locations, were recorded as the dependent variable. Participants' performances during the learning and the testing phases were examined respectively. We combined the data from the two configurations in the analysis as the data showed the same pattern for these two configurations in this experiment and in Experiment 2. In both Experiments, there is no interaction between the configurations and the learning-cue conditions on localization accuracy in either the last learning block or the testing blocks.

Performance during the learning phase. The learning effect was examined by mixed-model ANOVA on average response errors over the four learning blocks. Learning block (1-4) was a within-subject variable, whereas learning cue (L or B) was a between-subject variable. The analysis revealed an interaction between the learning cue and the learning block, F (3, 138) = 3.84, $p = .01$, $\eta_p^2 = .08$. Illustrated in Figure 2.3A, a larger learning effect in the L group contributes to the interaction. Repeated-measures ANOVA showed that participants in both groups improved their localization performances over the learning phase: for the L group, F (3, 69) = 9.19, $p < .001$, $\eta_p^2 = .29$, and for the B group, F (3, 69) = 4.10, $p = .01$, $\eta_p^2 = .15$.

Because of the learning effect, only the mean response errors in the last (i.e., fourth) learning block from the two conditions (L and B) were compared to ensure that participants were equally accurate at encoding individual locations relative to the respective cues. Performances were comparable between the two groups ($M_L = 20.05$ vm, $SD_L = 13.22$; $M_B = 19.82$ vm, $SD_B = 7.23$), F (1, 46) = .006, $p = .94$, $\eta_p^2 = .0001$ (Figure 2.4A).

Performance during the testing phase. The mean response errors during the testing phase as a function of the learning cue (L or B) were plotted in Figure 2.4A. Participants in L (M_L = 28.35 vm, SD_L = 15.04) were significantly more accurate than those in B (M_B = 55.60 vm, SD_B = 24.67), F (1, 46) = 21.36, $p < .001$, $\eta_p^2 = .32$. This result implies that the cognitive maps formed in the landmark group allowed a more accurate inference of the vectors between two objects' locations.

The deviation scores of individual response locations (calculated by subtracting the x-y coordinates of the correct target locations from those of the individual response locations) are plotted for both learning-cue conditions (Figure 2.5A). A smaller distance between one data point and the origin (0, 0) suggests higher accuracy of the corresponding response. The 95% confidence ellipses of the deviation scores and of the mean of the deviation scores are also plotted for both learning-cue conditions. The ellipses indicate that participants in either L or B group had no systematic response bias whereas responses in the B condition were more dispersed than those in the L condition, confirming that the cognitive map in the landmark group was more accurate.

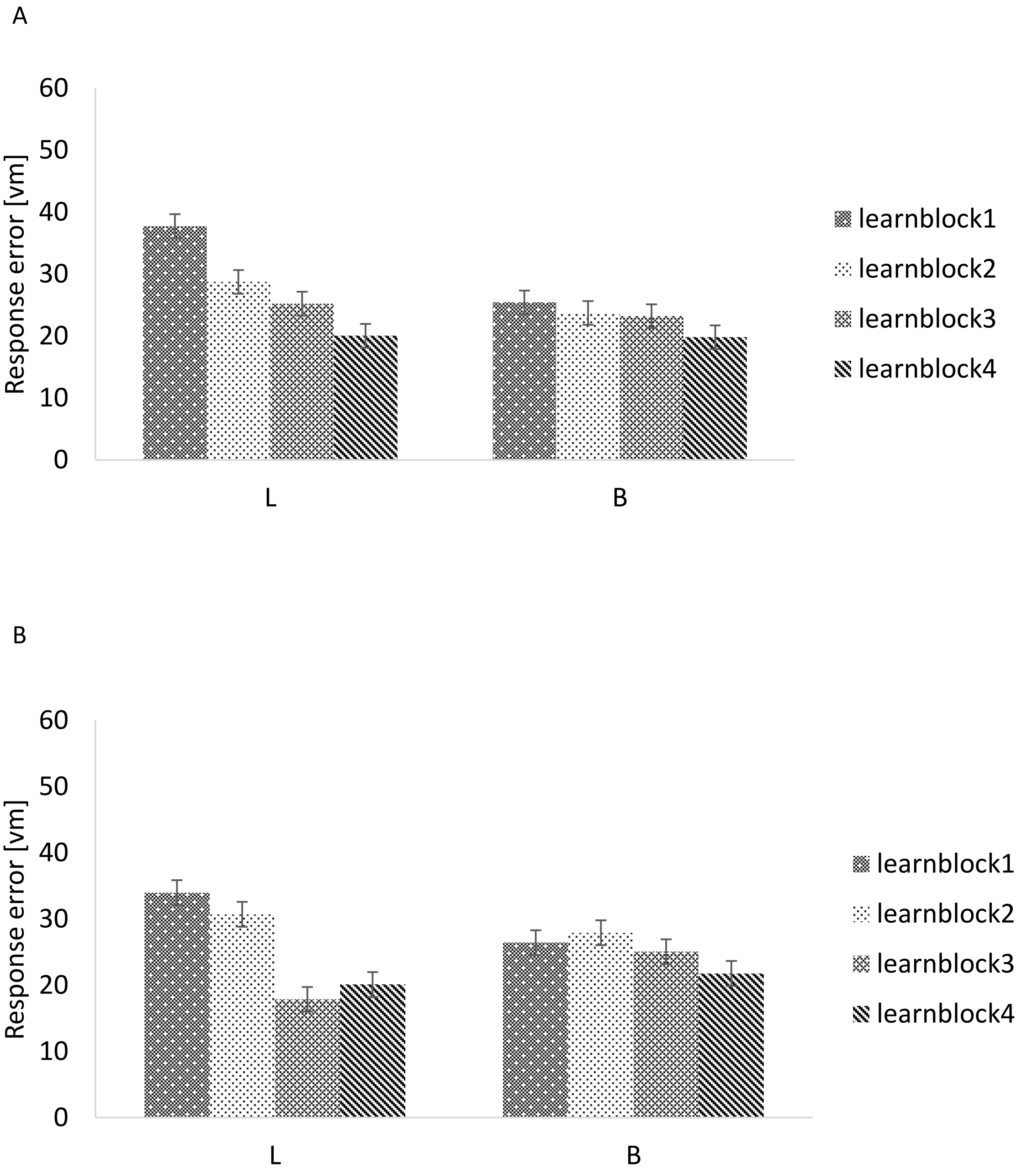


Figure 2.3. Response errors as a function of both the learning blocks (one to four) and the learning condition (L or B). A, in Experiment 1; B, in Experiment 2. Error bars are ± 1 standard error.

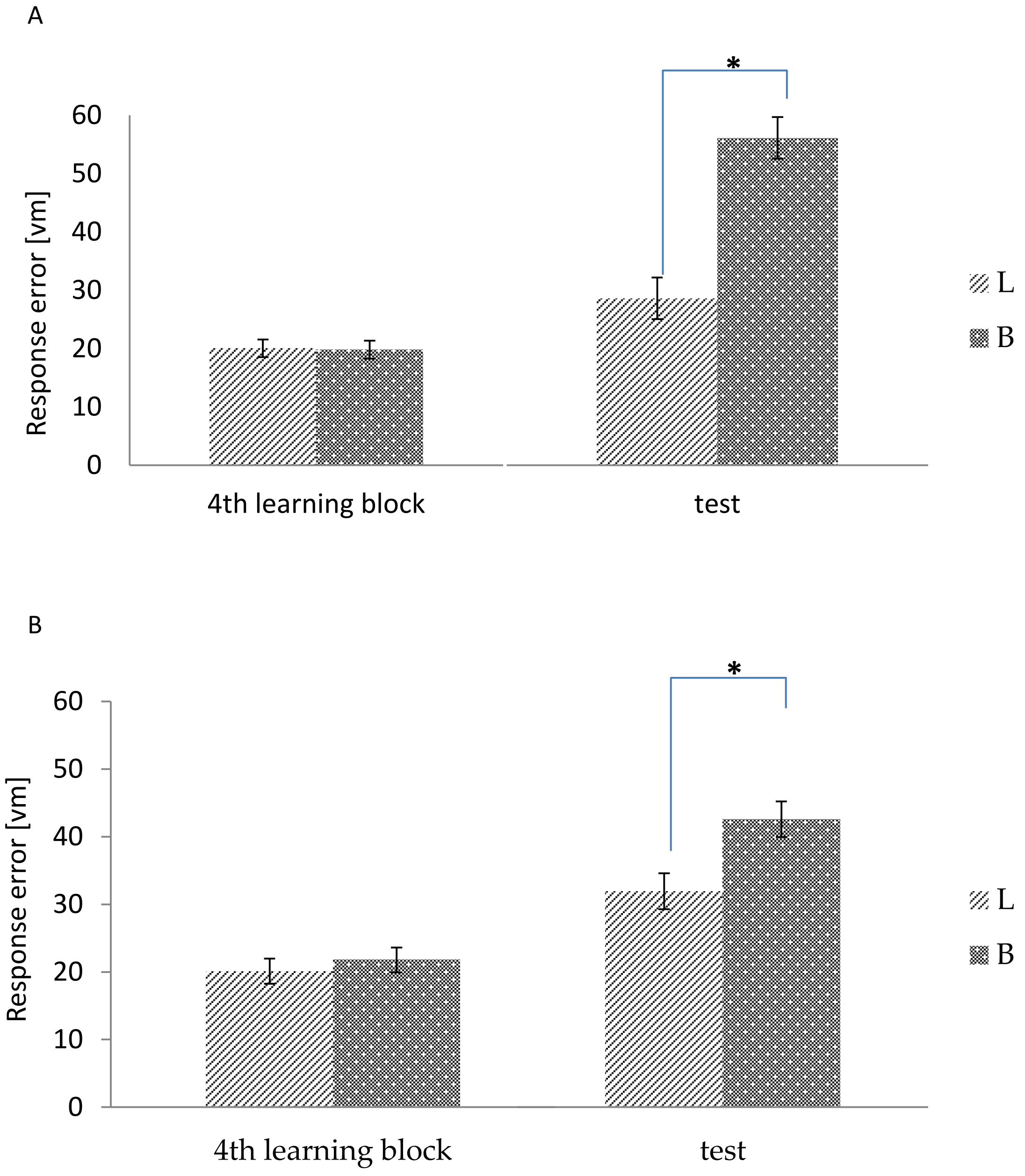
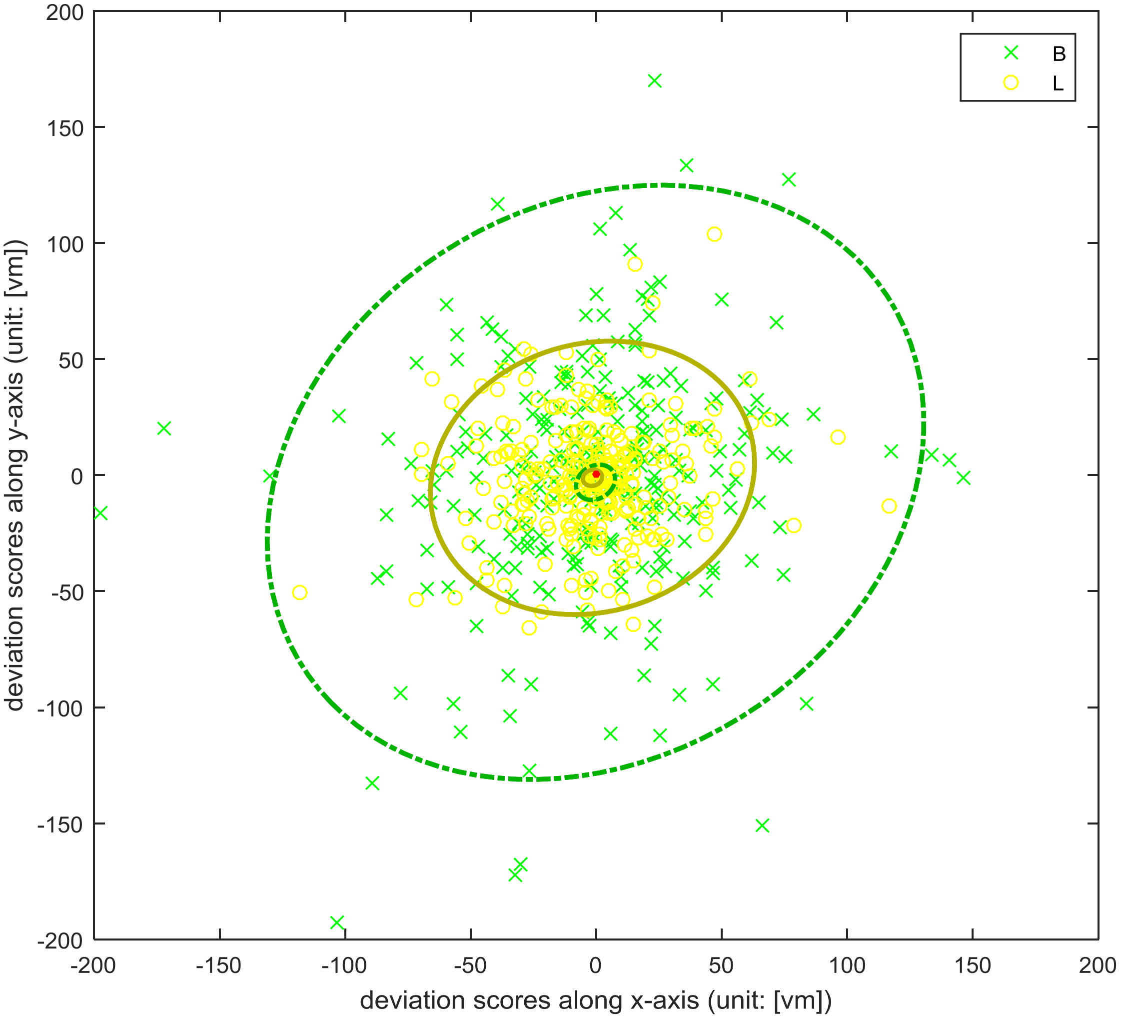


Figure 2.4. Response errors as a function of the learning condition (L or B) during the last (i.e. fourth) learning block and the testing phase, respectively. A, in Experiment 1; B, in Experiment 2. Error bars are ± 1 standard error.

A


B
L
200
150
100
50
0
-50
-100
-150
-200
-200
-150
-100
-50
0
50
100
150
200
deviation scores along y-axis (unit: [vm])
deviation scores along x-axis (unit: [vm])

B

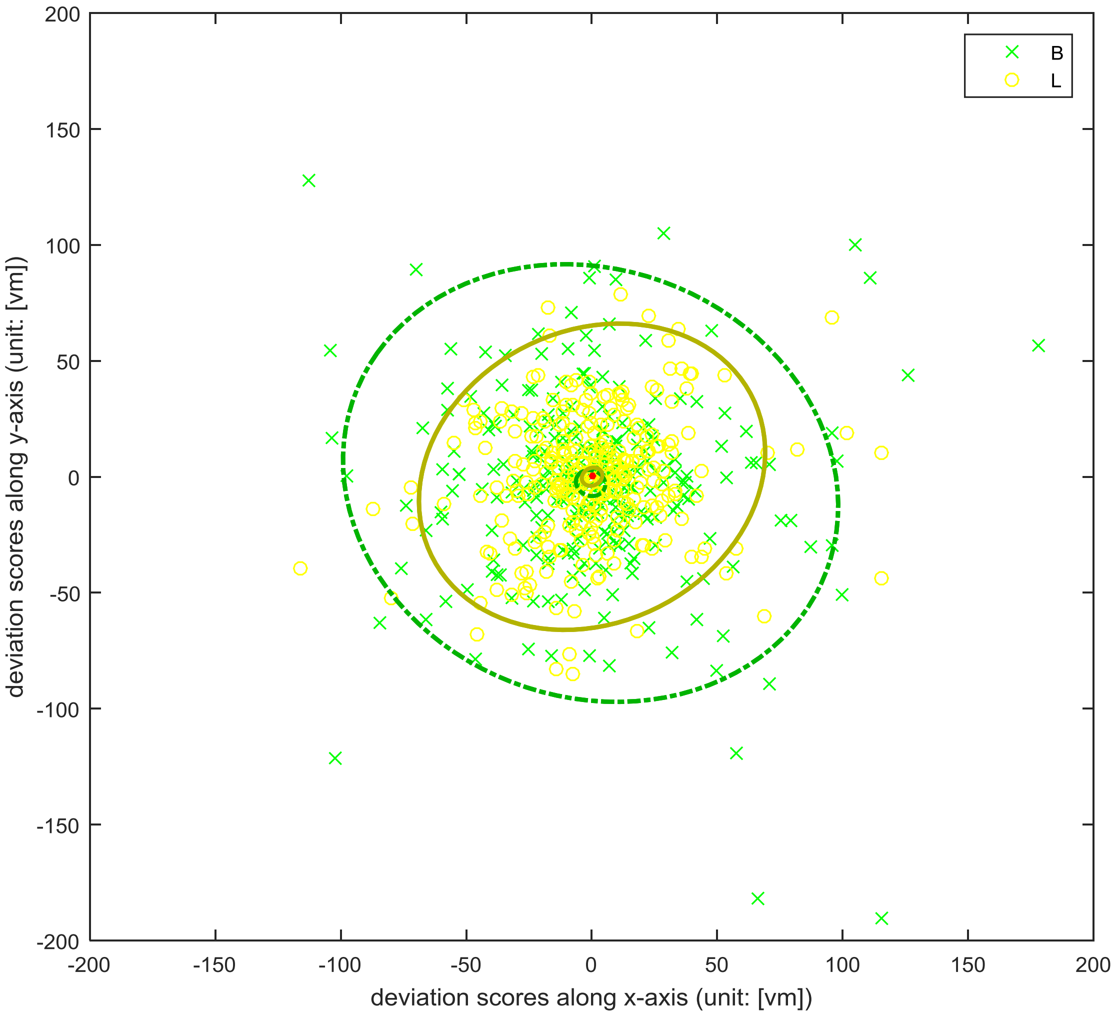


Figure 2.5. The deviations of all response locations from the correct location collapsed across the four objects and the 95% confidence ellipses of the individual deviations and of the mean of the individual deviations. The red dot at origin (0, 0) illustrates as the correct location. The green crosses represent all response deviations in the boundary condition. The yellow circles represent all response deviations in the landmark condition. The green ellipse in dashed line represents 95% confidence ellipses in the boundary condition (the large one is for the deviations and the small one is for the mean of the deviations). The yellow ellipse in solid line represents 95%

confidence ellipses in the landmark condition (the large one is for the deviations and the small one is for the mean of the deviations). A, in Experiment1; B, in Experiment 2.

2.4 Experiment 2

In Experiment 2, a task requiring inference of the spatial configuration among three objects was employed to evaluate the accuracy of the cognitive map of objects' locations in either learning-cue condition.

2.4.1 Method

Participants. Forty-eight students (24 males and 24 females) from the University of Alberta participated to fulfill a course requirement.

Materials, Design and Procedure. Experiment 2 was identical to Experiment 1 with the following exceptions. During testing, both the original localization cues (i.e. the wall, the traffic cone) and the distal orientation cues were removed. For each testing trial, two of the four objects were shown at their correct locations as the testing cues; participants replaced one of the other two objects. The combinations of six possible pairs of the cue objects and two possible probed objects for each cue pair yielded 12 testing trials.

2.4.2 Results and Discussion

Performance during the learning phase. Mixed-model ANOVAs were conducted on response errors across the four learning blocks to assess the learning effect. An interaction between the learning cue and the learning block was revealed, F (3, 138) = 5.67, p = .001, η_p^2 = .11. As shown in Figure 2.3B, the L group again had a larger learning effect. Repeated-measures ANOVA on the response errors revealed a learning effect in each condition (L or B): for the L group, F (3, 69) = 13.01, $p < .001$, $\eta_p^2 = .36$, and for the B group, F (3, 69) = 3.13, $p = .03$, $\eta_p^2 = .12$ (Figure 2.3B). Due to the learning effect, the response errors in the last learning block from the two conditions were compared. Localization accuracy did not differ between the two groups (M_L = 20.11 vm, SD_L = 15.73; M_B = 21.78 vm, SD_B = 9.23), F (1, 46) = 0.20, $p = .66$, $\eta_p^2 = .004$ (Figure 2.4B).

Performance during the testing phase. The mean response errors during the testing phase as a function of the learning cue (L or B) were plotted in Figure 2.4B. The participants in L (M_L = 31.68 vm, SD_L = 11.09) were more accurate than the participants in B (M_B = 42.24 vm, SD_B = 22.21), F (1, 46) = 4.35, $p = .043$, $\eta_p^2 = .09$. This result indicates that the cognitive map in the landmark group allowed a more accurate inference of the configurations among three objects' locations.

The deviation scores and the 95% confidence ellipses of the deviation scores and of the mean of the deviation scores are plotted for both learning-cue conditions (Figure 2.5B). The ellipses indicate that participants in either L or B group had no systematic response bias whereas responses in the B condition were more dispersed than those in the L condition, confirming that the cognitive map in the landmark group was more accurate.

2.5 General Discussion

The current study demonstrated that participants acquired a more accurate cognitive map through spatial learning relative to a single landmark than relative to a boundary. This cognitive map allowed participants to infer the vector between two objects' locations (Experiment 1) and the configuration among three objects' locations (Experiment 2).

These findings raise questions about the cognitive map theory because the cognitive map theory predicts the opposite pattern of results. We speculate that the cognitive map theory might be primarily applied to the representation of an object's location relative to a boundary. However, the representation of an object's location relative to another object, including a landmark, may not require hippocampus-dependent place learning. Although there is significant evidence showing that hippocampal place cells are sensitive to locations specified in terms of boundaries (O'Keefe & Burgess, 1996; for review see Barry et al., 2006), there is no direct evidence showing that hippocampal place cells are sensitive to locations specified relative to a landmark within the boundary (Cressant, Muller, & Poucet, 1997).

Our speculation is consistent with the proposal regarding the differential roles of hippocampus in different types of spatial memories. Nadel and Moscovitch (1997, see also Moscovitch et al., 2005) proposed that the hippocampus might be important to constructing detailed or episodic spatial memory, which consists of a rich context, whereas extra-hippocampal structures might be important to semantic spatial memory. In the current study, a boundary might have provided a rich context for locations within the boundary, whereas the metric relations between a location and a landmark might have lacked episodic or detailed information and therefore the representation of such spatial relations might be less hippocampal-dependent.

The vector addition model could well explain the current findings. This model conjectures that people can form a cognitive map as long as they encode metric relations of individual locations to a reference point regardless the learning mechanisms. Furthermore this model hypothesizes that people develop a better cognitive map when the locations are learned relative to one reference point than to multiple reference points. These conjectures are consistent with the findings of the current experiments. When participants encode four objects' locations relative to the boundary, they might use multiple pieces of the boundary from a variety of directions as reference points for each location, with the larger contribution from the closer boundary pieces (O'Keefe & Burgess, 1996; Hartley, Trinkler, & Burgess, 2004). Participants could select reference points on the homogeneous circular wall using the distal orientation cues. They might segment the wall into pieces and use the orientation cues to differentiate the wall segments (e.g. the wall segment close to Forest).

For simplicity, we assume that people only encode each location in terms of the closest boundary piece. Therefore, four different boundary pieces (reference points) are selected and four vectors between each object and the corresponding closest reference point are established. To infer the vector between any two objects, people have to add together the two reference-point-object vectors, as well as the vector between the corresponding reference points (e.g., Figure 2.1B). In contrast, when participants encode four objects' locations relative to a single landmark, the landmark serves as a common reference point and the inter-object vectors can be obtained by adding the two object-landmark vectors (e.g., Figure 2.1A). Because both encoding and adding the vectors between two reference points are prone to errors, participants in the boundary condition should have a less accurate cognitive map.

Compared with the cognitive map theory, the vector-addition model offers a better explanation for the current findings. However it is not the only possible explanation. One other possible explanation is that the homogeneous boundary could not have provided any visually distinctive reference point[1]. To specify a location, reference points as well as a reference

---

direction are required (Klatzky, 1998). According to this explanation, participants in the boundary condition might have inferred a reference point, e.g. the center of the boundary. This explanation further assumes that the initial mental representation of a target's location relative to the inferred reference point is comparable to the mental representation of the target's location relative to a visual landmark; however the spatial representation relative to the inferred reference point is less robust and decays more quickly than that relative to the landmark. Therefore, this explanation is consistent with the finding of the comparably accurate localization in the last learning block in both cue conditions but more accurate localization in the testing blocks in the landmark condition.

This explanation differs from the vector-addition model in terms of the way in which participants used the boundary to localize targets. According to the former one, participants inferred a less robust reference point whereas according to the latter, participants selected multiple reference points (Mou & Zhou, 2013). However both explanations predict less accurate cognitive mapping in the boundary condition, therefore challenging the cognitive map theory. Future studies are needed to distinguish these two explanations to further understand how people use a boundary to localize objects.

The finding that spatial learning relative to a landmark, rather than to a boundary, can lead to a better cognitive map strikingly contrasts with the superiority effect of a boundary cue over a landmark cue in learning individual locations when both cues were presented (Doeller & Burgess, 2008). This contrast indicates that the relative importance of a boundary cue and a landmark cue in spatial learning depends on encoding individual locations when both cues are present or inferring inter-location spatial relations after encoding individual locations with the presence of either cue.

We present evidence that a more accurate cognitive map for inferring inter-location spatial relations is acquired through learning individual locations relative to a single landmark than through learning individual locations relative to a boundary. We suggest that although spatial learning relative to a single landmark, compared to spatial learning relative to a boundary, might involve less place learning (i.e. more response learning) and depend less on the hippocampus (i.e. more on the striatum), because it involves encoding vectors between locations and the common reference (i.e. wall, traffic cone), it leads to a cognitive map; furthermore such representation is more accurate than that acquired through spatial learning relative to a boundary because cognitive mapping is more accurate relative to one reference point than to multiple reference points.

2.6 References

Aguirre, G. K., & D’Esposito, M. (1997). Environmental knowledge is subserved by separable dorsal/ventral neural areas. *The Journal of Neuroscience*, *17*(7), 2512-2518.

Barry, C., Lever, C., Hayman, R., Hartley, T., Burton, S., O’Keefe, J., Jeffery, H., & Burgess, N. (2006). The boundary vector cell model of place cell firing and spatial memory. *Reviews in the Neurosciences*, *17*(1-2), 71-97.

Bennett, A. T. D. (1996). Do animal have cognitive maps. *The Journal of Experimental Biology*, *199*, 219-224.

Bohbot, V. D., Kaline, M., Stepankova, K., Spackova, N., Petrides, M., & Nadel, L. (1998). Spatial memory deficits in patients with lesions to the right hippocampus and to the right parahippocampal cortex. *Neuropsychologia*, *36*(11), 1217-1238.

Corkin, S. (2002). What’s new with the amnesic patient H. M.? *Nature Reviews Neuroscience*, *3*, 153-160.

Cressant A., Muller, R. U., & Poucet, B. (1997). Failure of centrally placed objects to control the firing fields of hippocampal place cells. *The Journal of Neuroscience*, *17*, 2531–2542.

Doeller, C. F., & Burgess, N. (2008). Distinct error-correcting and incidental learning of location relative to landmarks and boundaries. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(15), 5909-5914.

Doeller, C. F., King, J. A., & Burgess, N. (2008). Parallel striatal and hippocampal systems for landmarks and boundaries in spatial memory. *Proceedings of the National Academy of Sciences of the United States of Americ*a, *105*(15), 5915-5920.

Ekstrom, A. D., Kahana, M. J., Caplan, J. B., Fields, T. A., Isham, E. A., Newman, E. L., & Fried, I. (2003). Cellular networks underlying human spatial navigation. *Nature*, *425*, 184-188.

Epstein, R. A., & Vass, L. K. (2014). Neural systems for landmark-based wayfinding in humans. *Philosophical Transactions of the Royal Society Biological Sciences*, *369*(1635), 20120533.

Evans, G. W., & Pezdek, K. (1980). Cognitive mapping: Knowledge of real world distance and location information. *Journal of Experimental Psychology: Human Learning and Memory*, *6*, 13-24.

Hartley, T., Maguire, E. A., Spiers, H. J., & Burgess, N. (2003). The well-worn route and the path less traveled: Distinct neural bases of route following and wayfinding in humans. *Neuron*, *37*, 877-888.

Hartley, T., Trinkler, I., & Burgess, N. (2004). Geometric determinants of human spatial memory. *Cognition*, *94*(1), 39-75.

Iaria, G., Petrides, M., Dagher, A., Pike B., & Bohbot, V. D. (2003). Cognitive strategies dependent on the hippocampus and caudate nucleus in human navigation: Variability and change with practice. *The Journal of Neuroscience*, *23*(13), 5945-5952.

Klatzky, R. L. (1998). Allocentric and egocentric spatial representations: Definitions, distinctions, and interconnections. In C. Freksa, C. Habel, & K. F. Wender (Eds.), *Spatial cognition - An interdisciplinary approach to representation and processing of spatial knowledge* (Lecture Notes in Artificial Intelligence 1404) (pp. 1-17). Berlin: Springer-Verlag.

Levine, M., Jankovic, I. N., & Palij, M. (1982). Principles of spatial problem solving. *Journal of Experimental Pscyhology: General*, *111*(2), 157-175.

Maguire, E. A., Nannery, R., & Spiers, H. J. (2006). Navigation around London by a taxi driver with bilateral hippocampal lesions. *Brain*, *129*, 2894-2907.

Marchette, S. A., Bakker, A., & Shelton, A. L. (2011). Cognitive mappers to creatures of habit: Differentail engagement of place and response learning mechanisms predicts human navigational behavior. *The Journal of Neuroscience*, *31*(43), 15264-15268.

McDonald, R. J., & White, N. M. (1994). Parallel information processing in the water maze: evidence for independent memory systems involving dorsal striatum and hippocampus. *Behavioral Neural Biology*, *61*(3), 260-270.

Miller, A. M., Vedder, L. C., Law, L. M., & Smith, D. M. (2014). Cues, context, and long-term memory: the role of the retrosplenial cortex in spatial cognition. *Frontiers in Human Neuroscience*, *8*: 586. doi: 10.3389/fnhum.2014.00586.

Moscovitch, M., Rosenbaum, R. S., Gilboa, A., Addis, D. R., Westmacott, R., Grady, C., McAndrews, M. P., Levine, B., Black, S., Winocur, G., & Nadel, L. (2005). Functional neuroanatomy of remote episodic, semantic and spatial memory: a unified account based on multiple trace theory. *Journal of Anatomy*, *207*, 35-66.

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), 1115-1127.

Nadel, L. (2013). Cognitive maps. In D. Waller & L. Nadel (Eds.), *Handbook of spatial cognition* (pp. 155-171). Washington, DC, US: American Psychological Association.

Nadel, L., & Moscovitch, M. (1997). Memory consolidation, retrograde amnesia and the hippocampal complex. *Current Opinion of Neurobiology*, *7*, 217–227.

O'Keefe, J., & Burgess, N. (1996). Geometric determinants of the place fields of hippocampal neurons. *Nature*, *381*, 425-428.

O'Keefe, J., & Dostrovsky, J. (1971). The hippocampus as a spatial map. Preliminary evidence from unit activity in the freely-moving rat. *Brain Research*, *34*, 171-175.

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

Pearce, J. M., Roberts, A. D. L., & Good, M. (1998). Hippocampal lesions disrupt navigation based on cognitive maps but not heading vectors. *Nature*, *396*, 75-77.

Siegel, A. W., & White, S. H. (1975). The development of spatial representations of large-scale environments. In H. W. Reese (Ed.), *Advances in child development and behavior* (Vol. 10, 9-55). New York: Academic Press.

Teng, E., & Squire, L. R. (1999). Memory for places learned long ago is intact after hippocampal damage. *Nature*, *400*, 675-677.

Thorndyke, P. W., & Hayes-Roth, B. (1982). Differences in spatial knowledge acquired from maps and navigation. *Cognitive Psychology*, *14*, 560-589.

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

Vass, L. K. & Epstein, R. A. (2013). Abstract representations of location and facing direction in the human brain. *The Journal of Neuroscience*, *33*(14), 6133-6142.

Wolbers, T., & Büchel, C. (2005). Dissociable retrosplenical and hippocampal contributions to successful formation of survey representations. *The Journal of Neuroscience*, *25*(13), 3333-3340.

Chapter 3

The limits of Boundary: Unpacking Localization and Cognitive Mapping Relative to a Boundary

3.1 Abstract

The studies in Chapter 2 (Zhou & Mou, 2016) showed that learning individual locations relative to a single landmark, compared to learning the locations relative to a homogenous circular boundary, led to a better cognitive map of these locations. The current study investigated whether the larger number of reference points would lead to a worse cognitive mapping and whether lack of direct spatial relations among the multiple reference points from a continuous boundary would also lead to a worse cognitive mapping relative to a boundary. We manipulated the number of primary reference points (one piece of ten-degree arc, four pieces of ten-degree arcs taken from a circular boundary or the complete boundary) available when participants were localizing four objects sequentially (Experiment 1) and the extendedness of each of the four arcs (Experiment 2). The results showed that cognitive mapping was less accurate in the order of one arc, four arcs, and the whole boundary. However expanding the size of each of the four arcs did not affect the accuracy of cognitive mapping until the four arcs were connected to form a continuous boundary. These findings indicate that when encoding individual locations relative to a homogenous circular boundary participants segmented the boundary into differentiating pieces and subsequently chose the most informative local part (i.e., the closest arc from the boundary to a location) as the primary reference point for a particular location. During this process the direct spatial relations among the reference points were likely unattended. These findings suggest that people might encode and represent bounded space in a fragmented fashion when localizing within in homogenous boundary.

3.2 Introduction

In daily life, we constantly travel between locations based on our knowledge of the spatial relations among the points of interest (e.g., getting from home to office). Often times the spatial relations between the locations are not directly learned but instead are inferred from our spatial representations of the environment built upon previous learning experience. Such representations that allow integrating metric representations of individual locations and inference of novel spatial relations are generally regarded as a form of cognitive map (Tolman, 1948; Bennett, 1996; Levine, Jankovic, & Palij, 1982; Nadel, 2013). In the current chapter, we refer to the process of integrating individual representations of locations (i.e., the vector between a target location and its reference point) to infer novel spatial relations as cognitive mapping.

Different environmental cues are proposed to contribute to the localization process (encoding individual locations) and the cognitive mapping process. In general, they are divided into two types. One type is a landmark cue based on discrete objects whereas the other type is a boundary cue based on continuous surfaces. These two cues are proposed to function differently in learning a single target location (Doeller & Burgess, 2008; Doeller, King, & Burgess, 2008). In particular, a landmark cue is involved in striatal-dependent response learning whereas a boundary cue is involved in hippocampus dependent place (latent) learning.

The study in Chapter 2 (Zhou & Mou, 2016) investigated whether the cognitive maps (i.e., knowledge of novel spatial relations among individual locations) derived from the two cues would also be qualitatively different. In that study, participants first learned the locations of four objects sequentially with either a circular wall or a single traffic-cone as the localization cue (distal orientation cues were provided in both conditions). They were subsequently tested on their knowledge of the spatial relations between two objects (Experiment 1) or of the spatial configuration among three objects (Experiment 2). The original localization cues (the traffic-cone or the whole wall) presented during the learning phase were removed during the testing phase; however, one of the four objects (Experiment 1) or two of the four (Experiment 2) were presented at its/their original location(s) (the distal orientation cues were still present during the testing phase). The testing tasks were thought to reflect the quality of the cognitive map of inter-location spatial relations derived from the respective cues (the boundary or the landmark) because participants had to infer novel spatial relations among the objects based on their memories. The results demonstrated a more accurate cognitive map (in terms of better knowledge about both novel spatial relations between two locations and spatial configurations among three locations) derived from a single landmark compared to that from a featureless circular wall. The finding is striking because it is believed that cognitive mapping relies on hippocampal-dependent place learning rather than striatal-dependent response learning (e.g., O’Keefe & Nadel, 1978; Tolman, 1948).

Previous studies (e.g., Doeller & Burgess, 2008) have shown that localization relative to a boundary cue involves place learning and is hippocampal dependent whereas localization relative to a single landmark involves response learning and is striatal-dependent. It is proposed that environmental boundaries or barriers are one of the major inputs to drive neural activities in the hippocampus of humans (Hartley, Trinkler & Burgess, 2004; Bird et al., 2010, for review, see Barry et al., 2006) and of rats (e.g., Hartley et al., 2000; Barry & Burgess, 2007). Combined with the theories (e.g., O’Keefe & Nadel, 1978) and the relevant findings demonstrating the critical role of hippocampal activities in forming cognitive maps of surrounding environment (Iaria, Petrides, Dagher, Pike, & Bohbot, 2003; Ekstrom, et al., 2003; Hartley, Maguire, Spiers,

& Burgess, 2003; Marchette, Bakker, & Shelton, 2011; McDonald & White, 1994; O'Keefe & Dostrovsky, 1971), one would expect that learning individual locations relative to a boundary should yield more accurate knowledge of inter-location spatial relations (i.e., a better cognitive map). However this prediction was inconsistent with the findings of Zhou and Mou (2016).

Zhou and Mou proposed a vector-addition model to articulate the cognitive mapping process. According to the model, when encoding a target location in the environment, one selects reference points from the available environmental cues and establishes a vector between the target location and its corresponding reference point. Furthermore, inference of inter-location spatial relations should be easier when the individual target locations are encoded relative to a common reference point than when the individual target locations are encoded relative to different reference points respectively. As illustrated in Figure 3.1A, to infer the vector $v_{a\text{-}b}$, between two points of interest a and b that are encoded to a common reference point R, one needs to add the vector between a and R, $v_{a\text{-}R}$, to the vector between b and R, $v_{b\text{-}R}$. As illustrated in Figure 3.1B, to infer the vector $v_{a\text{-}b}$ when a and b are encoded to two reference points R1 and R2 respectively, one needs to add three vectors together: the vector between a and R1 as denoted as $v_{a\text{-}R1}$, the vector between b and R2 as denoted as $v_{a\text{-}R2}$, and the vector between R1 and R2 as denoted as $v_{R1\text{-}R2}$. Zhou and Mou hypothesized that cognitive mapping was worse relative to the boundary because the circular boundary provided at least four non-overlapping reference points (i.e., different parts of the wall pieces) for encoding four individual locations, which resulted in a less accurate cognitive map of inter-location spatial relations. This account provided a starting point to understand why cognitive mapping relative to a homogenous circular boundary is a particularly challenging task. In the current study, we aimed to further unravel both the localization process and the cognitive mapping process relative to a homogenous circular boundary.

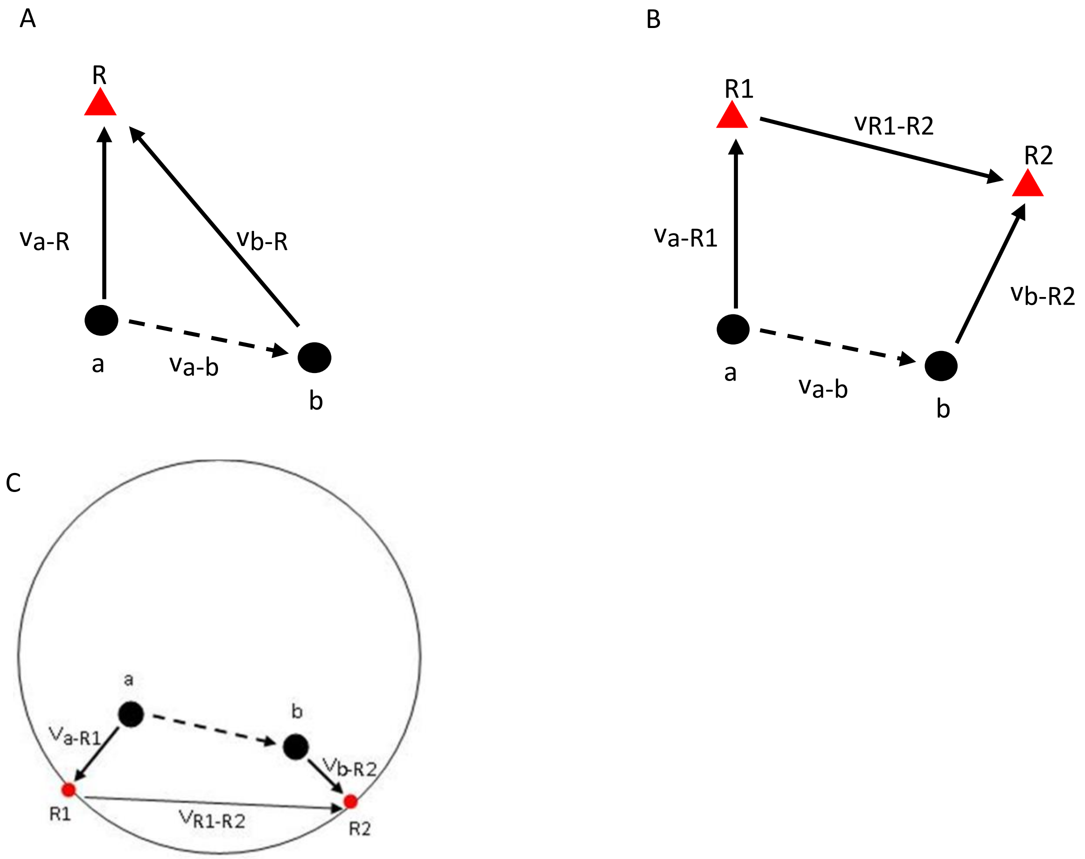


Figure 3.1. Schematic illustrations of the vector addition model. A, inferring the spatial relations between locations a and b when both locations are encoded relative to a single reference point R. The solid lines show the vectors from target locations to the reference point, $v_{a\text{-}R}$ and $v_{b\text{-}R}$. The dashed line shows the inferred vector between the two locations, $v_{a\text{-}b} = v_{a\text{-}R} + (-v_{b\text{-}R})$; B, inferring the spatial relations between locations a and b when a is encoded relative to the reference point R1 and b relative to R2. The solid lines with arrows show, respectively, the encoded vectors from a to R1 ($v_{a\text{-}R1}$), from R1 to R2 ($v_{R1\text{-}R2}$) and from b to R2 ($v_{b\text{-}R2}$). The dashed line shows the inferred vector between the two locations, $v_{a\text{-}b} = v_{a\text{-}R} + v_{R1\text{-}R2} + (-v_{b\text{-}R})$. C inferring the spatial

relation between locations a and b when a is encoded relative to a reference point, R1, segmented out and chosen from a circular boundary and b relative to a different reference point, R2, chosen from the boundary.

Following the vector-addition model proposed by Zhou and Mou (2016), we speculated two potential factors that might contribute to the difficulty in cognitive mapping process relative to a boundary. First is the number of the reference points. One chooses a part of the boundary (such as a wall segment that is close to a to-be-encoded location) as the reference point for encoding a particular location and different parts of the boundary are independently chosen when one learns different locations sequentially (e.g., R1 for a and R2 for b in Figure 3.1C). Thus, a circular boundary could be functionally equivalent to four separate wall segments when participants were learning four locations relative to the boundary in Zhou and Mou (2016). A cognitive map derived from four reference points is expected to be less accurate than that from a common reference point, which is the single landmark in Zhou and Mou (2016). Second, according to the vector-addition model, when multiple reference points are involved in encoding individual locations, knowing the spatial relations among the reference points (e.g., $v_{R1\text{-}R2}$ in Figure 3.1B) would be crucial to infer the inter-location spatial relations. Lack of such knowledge should impede cognitive mapping. In Zhou and Mou’s study, participants in the boundary group learned the four locations one at a time and were not aware of the spatial inference tasks during test. It is thus, very likely that the straight-line spatial relations between any two reference points were not directly encoded although participants knew the reference points were from the same circular wall. Note that these two factors are not mutually exclusive, either of them or the combination of the two would account for the worse cognitive maps derived from the homogenous circular wall.

Our speculation that a circular boundary, when presented as a localization cue for encoding individual objects, could be functionally equivalent to local wall pieces rather than a homogenous boundary as a whole fits well with the boundary vector cell (BVC) model proposed by Burgess and colleagues (Barry et al., 2006; Burgess, 2008). The boundary vector cell model postulates that place cells in the hippocampus receives inputs from an ensemble of the boundary vector cells that are responsive to the presence of a barrier at a given distance along a given allocentric direction. Furthermore, the degree of the control of a barrier over a BVC is positively correlated with the distance between the barrier and a moving organism's (in their model a rat's) location. Translating the BVC model to the behavioral level of a human localization task within a homogenous boundary, we hypothesize that participants first segment the boundary into multiple pieces (with the help of distal orientation cues) so as to discern different parts of the enclosed space (e.g., I'm close to the North section of the wall) (Mou & Zhou, 2013; see also Chapter 2). To encode a particular location, participants have then to choose the most informative segment of the boundary (i.e., the closest segment to the location), as the primary reference point to encode the location (by establishing the vector between this reference point and the location, such as the red points and the straight-line arrows illustrated in Figure 3.2). We refer to this wall segment as the optimal wall segment for that specific location. Therefore four optimal reference points (i.e., four wall segments) would be drawn from the whole boundary for four target locations. Meanwhile, the wall segments that are adjacent to the optimal segment could still have influence on the encoding of the same location but with reduced encoding resources assigned to them (such as the pink dots and the dotted-line arrows illustrated in Figure 3.2).

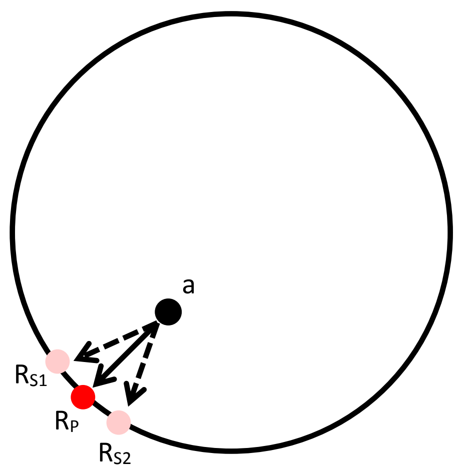


Figure 3.2. Schematic illustration of encoding a single location, a, relative to a homogenous circular boundary. The closest wall segment on the whole boundary to a is chosen as the primary reference points, as denoted as the red dot, R_P, in the figure. The straight-line arrow illustrates the vector established between a and R_P. In addition, the wall segments adjacent to the primary reference point (the optimal wall segment) would also contribute to the encoding/representation as the secondary reference points but with reduced input. Two example secondary reference points are illustrated as the pink dots, R_{S1} and R_{S2}. Two vectors were established between the two secondary reference points and a, illustrated as the two dotted-line arrows. The encodings of these two vectors would be assigned less computation resources than the one relative to R_P.

Experiment 1 examined the first factor, the number of reference points that might impede cognitive mapping relative to a homogenous circular boundary. The design was similar to that of Experiment 1 in Chapter 2. Participants learned the locations of four objects, one at a time, in three conditions differing in the localization cues available: one wall segment (ten degrees in central angle) taken from a homogeneous circular wall (Figure 3.3A), four wall segments from the circular wall (Figure 3.3B), and the complete circular wall (Figure 3.3C). The same distal orientation cues were provided in all three conditions. During the testing phase, the original localization cues were removed (the wall segments or the whole wall, respectively); however, the distal orientation cues still remained. One of the four objects was presented at its correct location while the other three objects were probed (Figure 3.3D). Thus, the cognitive map of the spatial relations among the four locations was assessed by the localization accuracy during the testing phase where novel spatial relations among the four objects had to be inferred.

The contrast in the cognitive mapping performance between the one-segment condition and the four-segment condition directly tested whether a larger number of reference points lead to a less cognitive map. If cognitive mapping relative to the four wall segments (multiple reference points) was shown to be less accurate than that relative to the one wall segment (a common reference point), the result would validate our assumption embedded in the vector-addition model that multiple non-overlapping reference points involved in encoding individual locations would lead to more complex vector-addition process to infer inter-location spatial relations, thus less accurate cognitive maps.

The comparison between the four-segment condition and the whole-wall condition tested whether a circular homogenous boundary would be treated as an inseparable unit or it would be functionally equivalent to four separate wall segments. If a circular homogenous boundary is treated as an inseparable unit, we would expect a better cognitive mapping process in the whole-wall condition than that in the four-segment condition because the circular wall treated as a whole unit might provide less reference points than the four segments do. If a circular homogenous boundary is functionally equivalent to four separate segments, we would expect equivalent cognitive mapping in these two conditions. Such a result would also explain the less accurate cognitive map derived from the whole boundary than that from the single landmark (Chapter 2; see also Zhou & Mou, 2016). Furthermore, as discussed in the segmentation hypothesis regarding localization relative to a homogeneous boundary, participants need to mentally segment out and choose an optimal reference point from the boundary for encoding each location whereas this segmentation and selection process was spared when there were already four separate wall segments available in the environment. Therefore locating four objects relative to the whole boundary could be more challenging compared to that relative to the four separate segments. Such challenge might even lead to less accurate encodings of the objects' locations (thus worse performance even in the learning phase of the whole-boundary condition compared to that of the four-segment condition), which in turn would yield less accurate cognitive maps.

Experiment 2 was mainly aimed to examine the second factor, that a lack of knowledge about the spatial relations among the reference points chosen from a homogenous circular boundary might impede cognitive mapping relative to the boundary. Participants learned the locations of four objects in terms of four segments drawn from a circular wall or in terms of the complete wall. They were then given the same cognitive mapping task as specified in Experiment 1. The size of each of the four wall segment was gradually increased across four conditions by increasing the central angle of each segment. The direct spatial relations among the wall segments were always perceivable when the separate four segments were presented simultaneously. If participants failed to encode and represent the direct spatial relations (such as the straight-line spatial relations) among the reference points chosen from the continuous wall, cognitive mapping performance would be less accurate in the complete-wall condition than in the four conditions of separate segments.

The contrasts among the four conditions of separate segments, which varied in terms of the horizontal size of each wall segment, could determine whether a primary reference point (optimal wall segments corresponding to individual locations) of a location is sufficient for encoding that location. If the primary reference point is sufficient, increasing the central angle of each segment should not affect either the encodings of individual locations or cognitive mapping of the locations.

3.3 Experiment 1

Participants learned four objects' locations, one at a time, with either one optimal wall segment (the size of which based on a central angle of ten degrees, Figure 3.3A) drawn from a circular wall (50 virtual meters in radius), four such optimal segments (Figure 3.3B), or the whole homogenous circular wall (Figure 3.3C). How the optimal wall segments were created will be elaborated in the sections below. A task requiring inference of the spatial relation between two objects was employed to evaluate the accuracy of the cognitive map of objects' locations in the above three conditions. The primary purpose of this experiment was to test whether the cognitive map derived from a larger number of reference points (e.g., four in the four-segment condition) would be less accurate than that derived from a smaller number (e.g., one in the one-segment condition). The secondary purpose was to test whether the continuous wall was treated as four reference points or an inseparable unit by comparing cognitive mapping performance in four-segment condition with that in the whole-wall condition.

3.3.1 Method

Participants. Seventy-two (36 males and 36 females) students from the University of Alberta participated to fulfill a course requirement.

Materials and Design. An immersive virtual environment was displayed using an nVisor SX60 head-mounted display (HMD) (NVIS Inc., Virginia). Graphics were rendered using the Vizard software (WorldViz, Santa Barbara, California). Head orientation was tracked with an InterSense IS-900 motion tracking system (InterSense Inc., Massachusetts). Thus, through head rotation, participants could change their viewpoints. Participants used a joystick to translate, to pick up and to place back the objects in the virtual environment.

In the virtual environment (see Figure 3.3), participants learned four locations on infinite grassland by picking up four sequentially presented objects (a candle, a lock, a bottle and a wood block) and then placing them at the correct locations. All participants learned the same set of four locations but the location-object pair was randomized across participants. Three groups of participants were randomly assigned to three difference learning-cue conditions. In all three learning-cue conditions, four different scenes (Ocean, Forest, Mountain and City) were set at infinity as distal orientation cues (indicated by the surrounding labels in Figure 3.3).

In the learning phase of the experiment, three different localization cues were presented according to the conditions: a homogenous circular wall with a radius of 50 virtual meters (vm), one wall segment drawn from the same circular wall and four wall segments from the circular wall. The first condition was referred to as B (Figure 3.3 C). The wall segments used in the latter two conditions are the wall segments which were closest to the four target locations compared to the remaining parts of the wall (each segment corresponding to one of the locations); the size of each piece was determined by a central angle of ten degrees. These four wall segments are also referred to as the optimal wall segments. To create one optimal wall segment, we first found the point (the size of which based on a central angle of zero degrees) on the whole wall that was closest in distance to one of the four to-be-learned locations. For each location, a line could be drawn to connect this location and the center of the circular wall and this line, when elongated, would intersect with the wall with two points. One of the two points would have the shortest distance to the particular location compared to all the other points on the wall, the other having the longest distance. Thus, we could get the four points on the wall closest to the four target locations correspondingly. Once getting such four points, we expanded the central angle of each point until each segment was ten degrees in central angle (five degrees expended to both the left side and the right side of the closest point) and each target location would then have a corresponding ten-degree optimal segment from the circular boundary. In the four-segment condition, all the four optimal segments were presented at the same time when participants were learning one of the four locations during each learning trial and we referred to this condition as 4OP (Figure 3.3B). Whereas in the one-segment condition, one of the four optimal segments (the same four used in 4OP) was randomly chosen to present to each participant but the same segment was presented throughout the learning phase for a particular participant; we refer to this condition as 1OP (Figure 3.3A). The localization cue in each condition (the wall segments in 1OP and 4OP, the circular wall in B) was presented throughout the learning phase only.

In the testing phase of the experiment (Figure 3.3D), the localization cues in the three conditions were removed; however, the distal orientation cues were still present. In addition, during each testing trial, one of the four objects was shown at its correct location to serve as the localization cue in the testing phase. Participants would have to replace the other three objects based on their inference of the spatial relations between the probed object and the cue object.

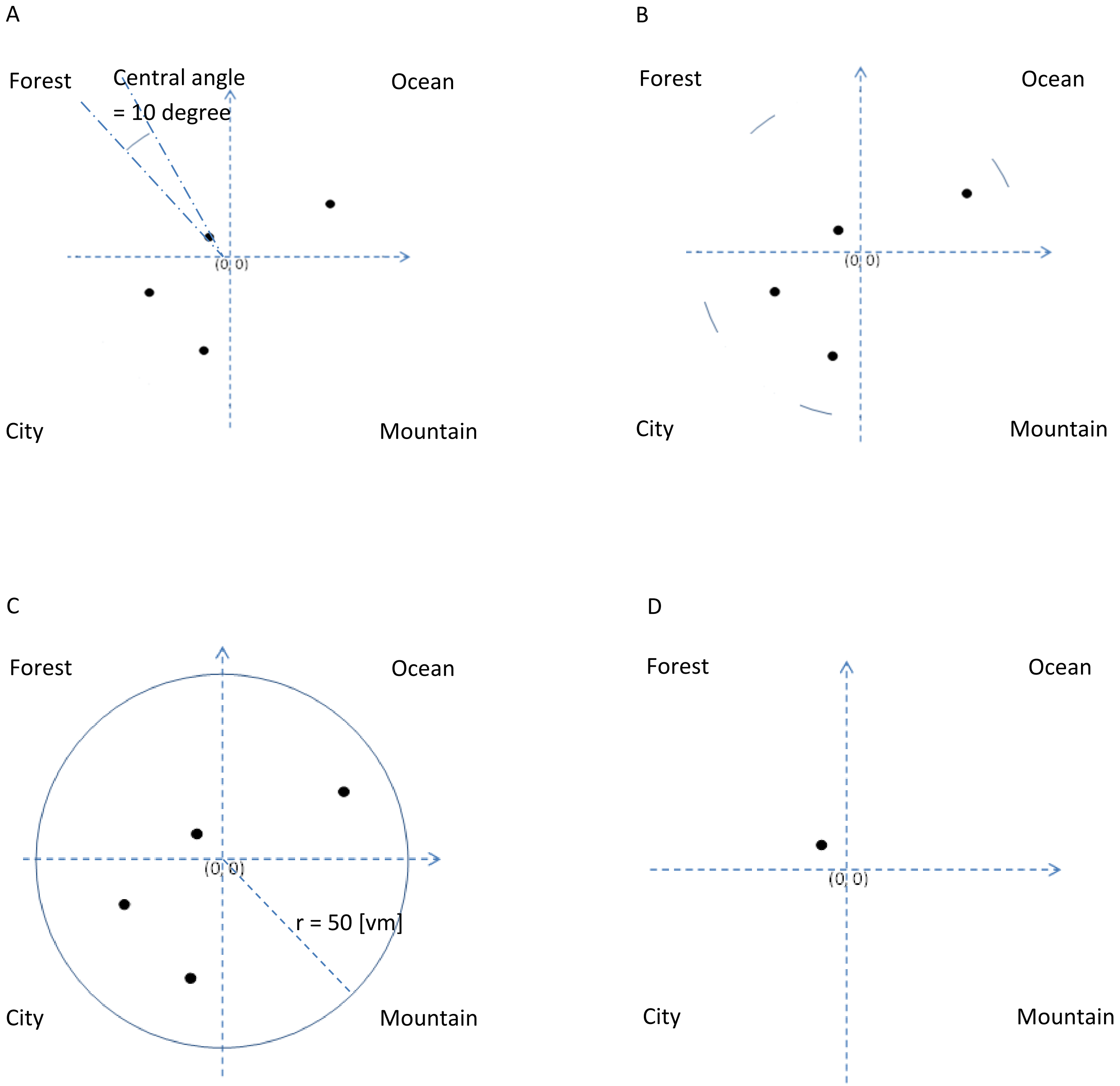


Figure 3.3. Top-view illustrations of the virtual environments used in Experiment 1. A, The learning phase of the one-optimal-segment condition (1OP). The arc illustrates one of the four optimal segments that would be shown to the participants, the size of which based on a central

angle of ten degrees (one of the four segments was randomly chosen for each participant but the same segment would be presented throughout the learning phase of that particular participant). The two dotted lines with arrows illustrate the coordinate axes where (0, 0) is the origin of the coordinate system (also the center of the wall) used in the virtual-reality environment. The axes, the center and the central angle are marked only for readers. The four dots illustrate the target locations used in both Experiment 1 and 2. The coordinates of the four target locations are (35.86, 19.88), (-7.74, -31.05), (-5.14, 6.13), (-18.02, -12.62) (units in vms). The four labels (Ocean, Mountain, City, and Forest) illustrate the background scenes set at infinity from the center of the environment; B, The learning phase of the four- segment condition (4OP). The four arcs illustrate the four optimal wall segments drawn from the circular wall, each being the closest of the wall to one of the four locations correspondingly; C, The learning phase of the whole-wall condition (B). The circle illustrates the homogenous circular wall, 50 virtual meters (vm) in radius; D, The testing phase in Experiment 1. The dot illustrates one of the four objects at its correct location presented as the testing cue for one particular trial. The original localization cue (the single wall segment, the four wall segments or the boundary) was removed however the distal orientation cues were retained.

Procedure. Participants donned the HMD and sat on a swivel chair at the center of the experiment room. Each participant went through three phases: the pick-up phase, the learning phase and the testing phase. During the pick-up phase, participants collected the four objects one by one from their original locations (only one object appeared at its correct location for participants to collect each time). The environment of the pick-up phase was the same as that of the learning phase. The learning phase comprised four blocks of four learning trials (one trial per object in each block). During each learning trial, one of the four objects was probed and participants replaced the probed object based on their memory of its original location. After the response, the probed object appeared at its correct location (feedback). Participants were asked to collect it. Participants' starting locations (could be anywhere within 40 virtual meters from the center of the wall used in B) and their facing directions at the beginning of each trial were randomized. During testing, the boundary in B and the separate wall segments in 1OP/4OP were removed. During each testing trial, one of the four objects was shown at its correct location as a localization cue together with the distal orientation cues; participants replaced one of the other three objects. The testing phase comprised four blocks of three testing trials. In each block, one of the four objects served as the testing cue in all three trials and each of the other three objects was probed once. No feedback was given in the testing phase.

3.3.2 Results and Discussion

Response errors, as measured by the distance between each of participants' response locations and the corresponding correct location, were recorded as the dependent variable. We examined participants' localization performance during the learning phase and the testing phase separately.

Performance during the learning phase. The learning effect was examined by mixed-model ANOVAs on mean response errors over the four learning blocks. Learning block (1-4) was a within-subject variable, whereas learning cue (1OP, 4OP and B) was a between-subject variable. A main effect of learning block was revealed, $F_{(3, 207)} = 19.69, p < .001, \eta_p^2 = .22$; there was no interaction between learning cue condition and learning block, $F_{(6, 207)} = .52, p = .79, \eta_p^2 = .02$.

Hence participants in all three groups improved their localization accuracy in terms of placing the objects with respective cues in the environment (Figure 3.4A).

The mean response errors in the fourth learning block from the three conditions (1OP, 4OP and B) were compared. The one-way ANOVA analysis revealed an effect of learning cue condition (Figure 3.4B), $F_{(2, 69)} = 3.35$, $p = .041$, $\eta_p^2 = .09$. Pairwise comparisons demonstrated that participants in the 4OP group ($M_{4OP} = 15.44$ vm, $SD_{4OP} = 7.11$, units in virtual meters [vm]) were more accurate replacing the objects than those in the 1OP condition ($M_{1OP} = 21.60$ vm, $SD_{1OP} = 11.65$), $t_{(69)} = 2.37$, $p = .02$, Cohen's $d = .68$, and as well as those in the B condition ($M_B = 20.86$ vm, $SD_B = 7.52$), $t_{(69)} = 2.09$, $p = .04$, Cohen's $d = .60$. The localization accuracy in the 1OP group was comparable to that in the B group, $t_{(69)} = .29$, $p = .78$, Cohen's $d = .08$.

Performance during the testing phase. The mean response errors during the testing phase as a function of the learning cue (1OP, 4OP and B) were plotted in Figure 3.4B. One-way ANOVA revealed an effect of learning cue condition: the accuracy of inferring spatial relations among the objects differed in the three groups, $F_{(2, 69)} = 8.13$, $p = .001$, $\eta_p^2 = .19$, suggesting that the cognitive maps of inter-object spatial relations derived from the three cues were different. Pairwise comparisons demonstrated that participants in the B condition ($M_B = 51.25$ vm, $SD_B = 27.50$) were less accurate inferring the inter-object spatial relations than those in the 1OP group ($M_{1OP} = 30.20$ vm, $SD_{1OP} = 10.54$), $t_{(69)} = 3.85$, $p < .001$, Cohen's $d = 1.11$, and also less accurate than those in the 4OP condition ($M_{4OP} = 34.98$ vm, $SD_{4OP} = 14.52$), $t_{(69)} = 2.97$, $p = .004$, Cohen's $d = 0.86$. Meanwhile participants in the 1OP and the 4OP condition were equivalently accurate in inferring spatial relations among the objects, $t_{(69)} = .87$, $p = .39$, Cohen's $d = .25$.

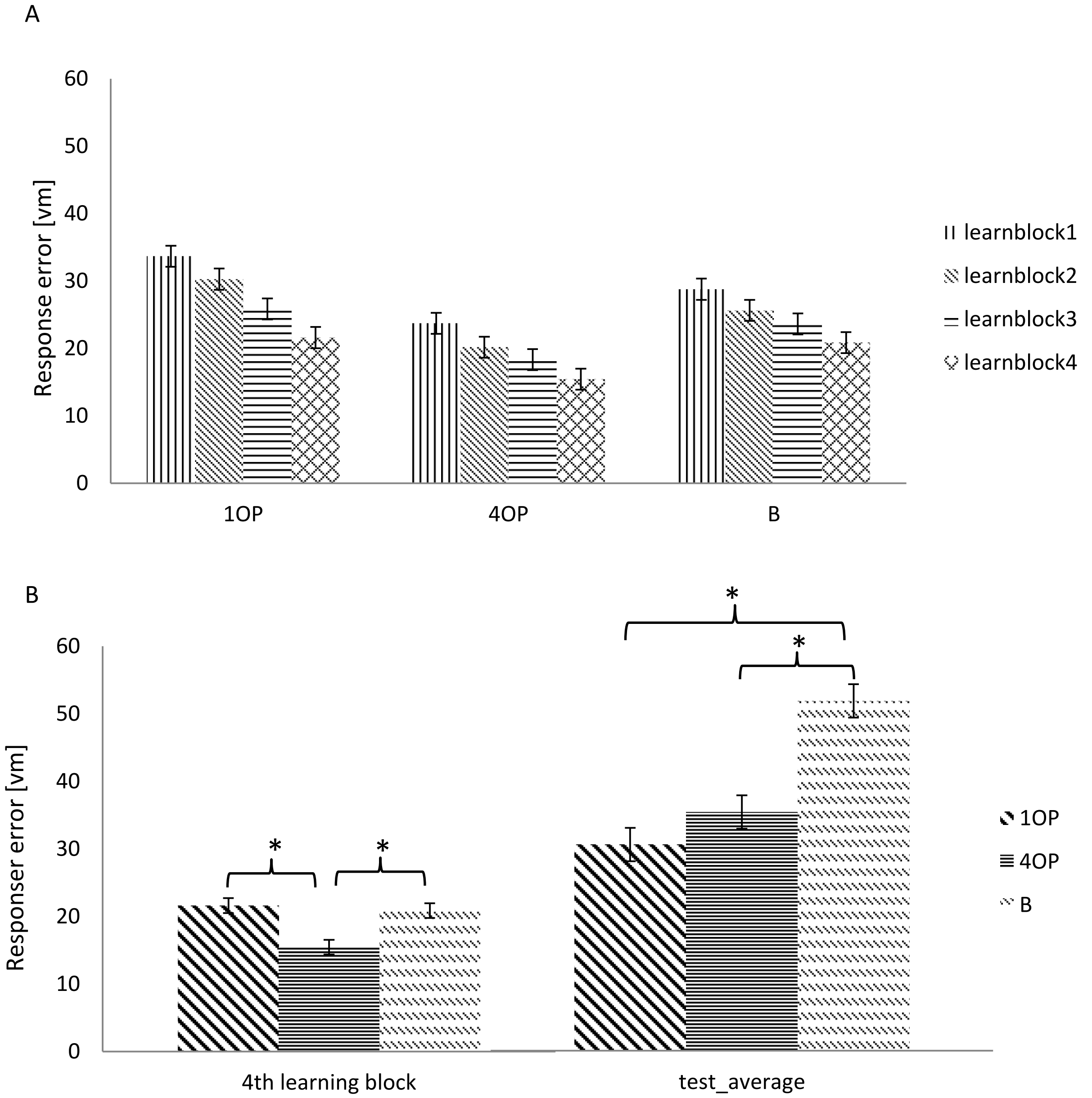


Figure 3.4. Response errors during the learning phase and the testing phase in Experiment 1. A, Response errors during the learning phase as a function of both the learning blocks (one to four) and the learning-cue condition. The learning-cue conditions were 1OP, 4OP and B; B, Response errors as a function of the learning-cue condition during the last (i.e. fourth) learning block and during the testing phase, respectively. Error bars are ± 1 standard error.

The comparison between the 1OP and the B conditions replicated the finding in our previous study that learning individual locations relative to a homogeneous circular boundary led to a less accurate cognitive map than learning locations relative to a single landmark. Hence one piece wall segment (ten degrees in central angle) provided a common reference point for encoding the four objects' locations, which benefits integrating the representations of the individual locations into a cognitive map of inter-location spatial relations.

Learning-testing discrepancy in localization performance. To examine whether the difference in localization during testing was due solely to the difference in localization during learning, mixed-model ANOVAs were performed with experiment phase (the learning phase vs. the testing phase) as a within-subject variable and learning cue (1OP, 4OP and B) as a between-subject variable.

The mixed-model ANOVAs showed an overall interaction between learning phase and learning cue, $F_{(2,\,69)} = 6.88$, $p = .002$, $\eta_p^2 = .17$, suggesting that there was varying discrepancy between learning and testing performance depending on the learning cue condition. Three sets of simple contrasts were carried out to unpacking the overall interaction effect, more specifically the learning-testing discrepancies between the 1OP and the 4OP condition, between the 1OP and the B condition, between the 4OP and the B condition respectively. As revealed by the analysis, the overall interaction mainly was driven by the larger learning-testing discrepancy in localization performance in the B condition than that in the 1OP condition, $F_{(1,\,69)} = 13.76$, $p < .001$, $\eta_p^2 = .17$. There was a trend of larger learning-testing discrepancy in the whole-boundary condition than that in the four-segment condition, $F_{(1,\,69)} = 3.41$, $p = .07$, $\eta_p^2 = .05$, and as well as a trend of larger learning-testing discrepancy in the four-segment condition than that in the in the one-segment condition, $F_{(1, 69)} = 3.47$, $p = .07$, $\eta_p^2 = .05$. Hence it is tempting to hypothesize that the less accurate cognitive map of inter-location spatial relations derived from the boundary was not solely due to the less accurate representations of individual locations relative to the boundary but there were other contributing factors that impeded cognitive mapping relative to the homogenous circular wall.

As revealed in the above analysis, localization in the learning phase was worse in the 1OP condition than in the 4OP condition although localization in the testing phase in these two conditions was comparable. This demonstrated that using the common reference point for the four objects' locations enables participants to integrate the representations of those locations into a cognitive map more easily than using separate reference points. Therefore it is consistent with the vector addition model in that the more non-overlapping reference points involved in encoding individual locations would lead to a less accurate cognitive map of these locations.

The less accurate localization in both the testing and the learning phase of the B condition, and the fact that there was a larger learning-testing discrepancy in the B condition than in the 4OP condition, indicate that the homogenous circular wall was not equivalent to four optimal wall segments. In particular, integrating representations of individual locations relative to the homogenous circular wall were more difficult. There could be two reasons. First, participants might have chosen more than four reference points in the B condition. In this case people would still choose one optimal wall segment as the major reference point for encoding each location but they could also pick other segments as the secondary reference points for the same location. Thus, for each location, participants could have multiple reference points; as a result, integrating the locations into a cognitive map would be more complicated, leading to less accurate knowledge of inter-location spatial relations. Secondly when learning the four locations sequentially relative to a featureless circular wall, participants would never have the chance to perceive the four major reference points (i.e. the four optimal reference points they had chosen) at the same time because they would only identify each optimal segment every time they were localizing one of the four objects. Consequently, the knowledge of the spatial relations among the reference points was limited in the whole-wall condition, which hindered cognitive mapping of the four locations. Experiment 2 was designed to dissociate these two possibilities.

3.4 Experiment 2

In Experiment 2, we aimed to test the two possibilities that might explain the fact that cognitive maps derived from a homogenous circular wall were less accurate than those derived from four separate wall segments: 1) the secondary reference points for encoding individual locations (and their associated vectors to the locations) were significantly involved in the vector-addition process for inferring inter-location spatial relations in the whole-wall condition, leading to a more complex integration process; 2) the lack of knowledge of the direct spatial relations among the chosen reference points (i.e., the optimal wall segments) would impair inference of inter-location spatial relations.

To test the first possibility, we retained the 4OP condition used in Experiment 1 (four optimal wall segments, the size of each segment based on a central angle of ten degrees, were presented during the learning phase as the localization cue) and enlarged the central angle of each segment to create another three conditions where the extendedness of the wall-segment array was increased across the conditions (Figure 3.5A-C). Through this manipulation, we expected to increase the number of potential reference points available in the environment for localizing each object, making it more likely that participants would choose the secondary reference points given the increase in the extendedness of the wall-segment arrays. If the secondary reference points were involved in the vector addition process for inferring the inter-object spatial relations, we would expect decreased accuracy in localization performance during the testing phase as a result of increasing the central angle of each optimal wall segment across the conditions.

To test the second possibility, a fifth condition was employed where both the original circular wall (the same one used in Experiment 1) and one of the four optimal ten-degree wall segment placed on top of the wall were presented during each learning trial (Figure 3.5D). Hence participants in this condition would also see the optimal wall segment directly but never see the four separate segments simultaneously.

3.4.1 Method

Participants. 120 (60 males and 60 females) students from the University of Alberta participated to fulfill a course requirement.

Materials, Design and Procedure. The overall paradigm in Experiment 2 is the same as that in Experiment 1 with the following exceptions.

Five conditions were employed where different environmental cues were presented as the localization cues during the learning phase. The first learning condition was identical to the four-optimal-segment condition used in Experiment 1 and we refer to this condition as 4OP_10 in the current experiment. The other two learning conditions were created by increasing the central angle of each segment in the 4OP_10 condition to 20 degrees (referred to as 4OP_20, Figure

3.5A) and to 30 degrees respectively (referred to as 4OP_30, Figure 3.5B). We enlarged the central angle of each ten-degree segment by extending the original angle by five degrees (in the 4OP_20 condition) and ten degrees (in the 4OP_30 condition) both clockwise and counterclockwise. For the fourth condition, instead of extending the size of the wall segments in the 4OP_10 condition, we removed four wall segments (ten degrees in central angle) from the whole circular wall used in Experiment 1 such that the array of the remaining segments provided the largest number of potential reference points compared to the first three conditions. We referred to this condition as 4C (the letter C stands for cuts which means four ten-degree wall segments were cut out from the circular wall, Figure 3.5C). Each segment removed was the segment of the whole wall located furthest away from a corresponding object. As mentioned in the Method section of Experiment 1, the line connecting one target location and the center of the wall intersected the circular wall at two points. The closer point of the two was the point on the wall closest to this particular location, and the farther one was the point on the wall farthest from the target location. Thus, we obtained four farthest points for the four locations; each of these points could be regarded as a wall segment with zero degrees in central angle. By enlarging the central angle of each farthest point to ten degrees (five degrees clockwise and five degrees counterclockwise), we were able to get four ten-degree wall segments which were furthest away to the four objects' locations (one corresponding to one of the four locations). These four segments were then removed from the circular wall to create the array used in 4C.

The last condition was employed to test whether limited knowledge of the direct spatial relations among the reference points chosen from a homogenous circular wall impede cognitive mapping relative to the wall. We hypothesize that participants were only focusing their attention on one optimal wall segment when they were locating one object, as it would be the most informative reference point for encoding the location of the current object. Hence the whole circular wall could be regarded as one wall segment during one learning trial and as four sequentially presented segments through four successive trials when participants learned four objects' locations sequentially. Contrary to the conditions where four segments were presented simultaneously, participants might not have been aware of the direct spatial relations among the reference points on the homogenous boundary. To mimic this localization process in the homogenous circular wall condition, we placed one of the four optimal segments (the same four used in 4OP_10) on top of the whole circular wall (the same wall used in B in Experiment 1) when participants were learning one of the four locations during each learning trial (the optimal segment on top was always the closest to the target location during a particular trial). Across successive learning trials involving the task of locating different objects, participants would see four different higher segments (though not simultaneously) together with the original circular wall. Hence the optimal reference points for the four locations were made more salient compared to the remainder of the wall. We referred to this last condition as 1OPB_10 (Figure 3.5D). We anticipated that cognitive mapping performance (i.e., knowledge of inter-object spatial relations) in 1OPB_10 would be comparable to that relative to the circular wall, and less accurate than those in the first four conditions, where direct spatial relations among the optimal segments (such as forming a shape among the four separate segments) were perceivable. Furthermore, because the optimal reference points were made much more salient by having one of the four segments higher than the remainder of the wall during each learning trial, the localization performance in the learning phase of 1OPB_10 would be better than that relative to the homogenous circular wall alone (given that participants could spare the mental effort of segmenting and choosing the appropriate optimal reference points). We also expected the localization performance in the last condition to be equivalent to those in the first four conditions.

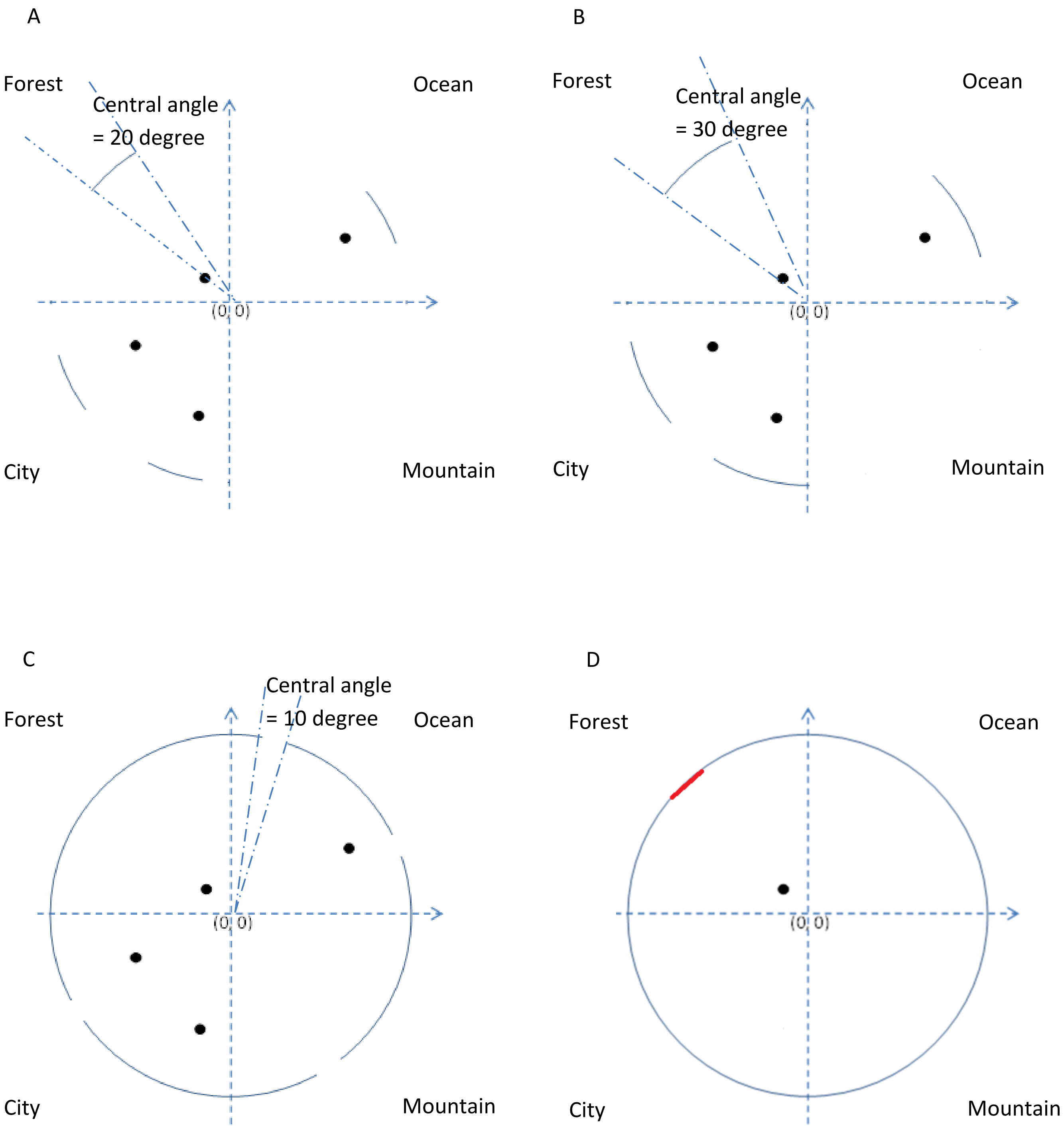


Figure 3.5. Top-view illustrations of the virtual environments used in Experiment 2. A, The learning phase of the four-segment condition where each segment had a central angle of twenty degrees (4OP_20). The four arcs illustrate the four optimal wall segments, the size of each based

on a central angle of twenty degrees; B, The learning phase of the four-segment condition where each segment had a central angle of thirty degrees (4OP_30). The four arcs illustrate the four optimal segments, the size of each based on a central angle of thirty degrees; C, The learning phase of the four-segment condition in which the four segments of the wall furthest from the four locations were cut out (4C). Each cut-out segment had a central angle of ten degrees; D, The learning phase of the condition where the whole wall, together with one of the four optimal ten-degree segments on top of the wall, was presented in each trial (1OPB_10). Different optimal segments would be presented on top of the wall, corresponding to the location to be learned in a particular trial. The red arc illustrates one particular optimal segment on the top of the circular wall in a particular trial when participants were replacing an object, the correct location of which was at (-5.14, 6.13) (illustrated as the black dot).

3.4.2 Results and Discussion

As in Experiment 1, response error was used as the dependent variable to indicate the localization performance in the learning phase, which involves locating individual objects, and the knowledge of inter-object spatial relations in the testing phase.

Performance during the learning phase. The mixed-model ANOVAs were carried out on the averaged response errors across four trials in each learning block to examine the learning effect across the four blocks. Learning-cue condition (4OP_10, 4OP_20, 4OP_30, 4C vs. 1OPB_10) was the between-subject variable and learning block (1-4) was the within-subject variable. The analysis revealed a main effect of learning block, $F_{(3, 345)} = 31.13$, $p < .001$, $\eta_p^2 = .21$, but no effect of learning-cue condition, $F_{(4, 115)} = 1.32$, $p = .27$, $\eta_p^2 = .04$, nor an interaction between the two variables, $F_{(12, 345)} = .83$, $p = .62$, $\eta_p^2 = .03$. The mean response errors of locating the four objects across the four blocks for each learning cue condition was plotted in Figure 3.6A. As shown in the figure, the mean response errors decreased as the learning phase progressed, indicating that knowledge of individual locations relative to the respective localization cues available in each condition was improved.

Again we compared participants' performance in the last learning block across all conditions to examine whether representations of individual locations relative to respective environmental cues were equally accurate. A one-way ANOVA was carried out on the mean response errors in the fourth block across the five conditions (4OP_10, 4OP_20, 4OP_30, 4C and 1OPB_10, Figure 3.6B). The analysis revealed no effect of learning-cue conditions, $F_{(4, 115)} = 1.18$, $p = .32$, $\eta_p^2 = .04$. Thus, the representations of the four objects' locations relative to the respective cues in the five conditions were considered to be qualitatively comparable.

Performance during the testing phase. A one-way ANOVA was carried out on the mean response errors (averaged across all the trials in the testing phase) to examine the quality of cognitive maps derived from respective cues in the five conditions (Figure 3.6B). A main effect of learning-cue condition was revealed, $F_{(4, 115)} = 4.23$, $p = .003$, $\eta_p^2 = .13$. Post-hoc comparisons showed that localization performances were equivalent across 4OP_10 (M = 40.58 vm, SD = 11.18), 4OP_20 (M = 38.01 vm, SD = 18.22), 4OP_30 (M = 37.81 vm, SD = 14.16) and 4C (M = 38.47 vm, SD = 14.72). However localization performance was worse in the 1OPB_10 condition than in the other four, $t_{1OPB\_10 \text{ vs. } 4OP\_10} = 2.83$, $p = 0.006$, Cohen's $d = 0.82$; $t_{1OPB\_10 \text{ vs. } 4OP\_20} = 3.36$, $p = 0.001$, Cohen's $d = 0.97$; $t_{1OPB\_10 \text{ vs. } 4OP\_30} = 3.40$, $p < 0.001$, Cohen's $d = 0.98$; $t_{1OPB\_10 \text{ vs. } 4C} = 3.26$, $p = 0.001$, Cohen's $d = 0.94$. Hence participants' knowledge of inter-location spatial relations was less accurate when they were learning individual locations relative to the optimal segments with minimal knowledge of the direct spatial relations among these segments; whereas such knowledge was maintained when the direct spatial relations among the optimal reference points were perceivable (i.e., when the four separate segments were presented simultaneously). The results supported the speculation that limited knowledge of the direct spatial relations among the reference points chosen from a homogenous circular boundary impedes cognitive mapping relative to the boundary.

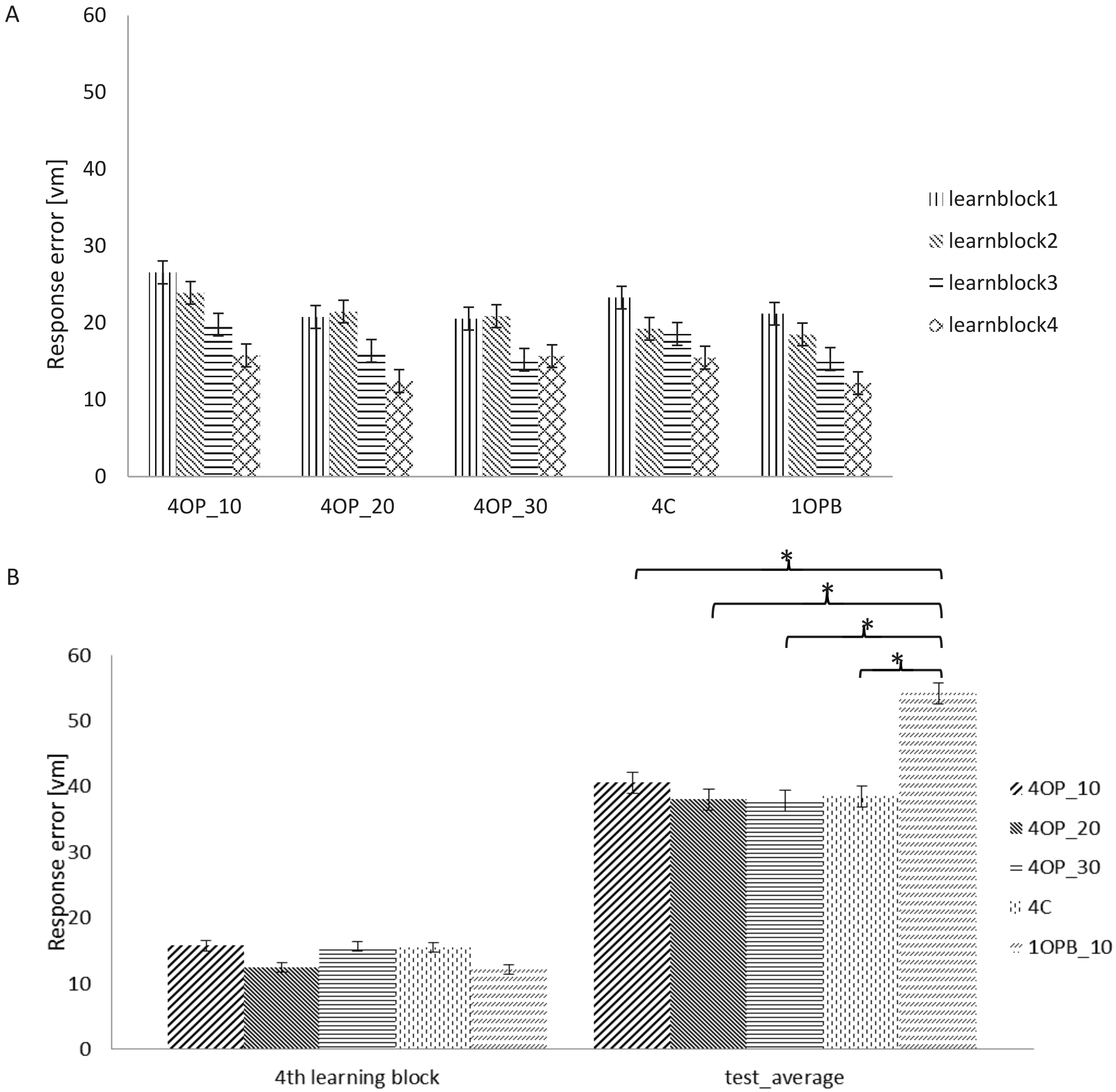


Figure 3.6. Response errors during the learning phase and the testing phase in Experiment 2. A, Response errors during the learning phase as a function of both learning blocks (one to four) and learning-cue conditions. The learning-cue conditions were 4OP_10, 4OP_20, 4OP_30, 4C and 1OPB_10 respectively; B, Response errors as a function of the learning-cue condition during the last (i.e. fourth) learning block and during the testing phase, respectively. Error bars are ± 1 standard error.

3.5 General Discussion

Two experiments investigated the factors that impede cognitive mapping relative to a homogenous circular boundary, as distinct from cognitive mapping relative to the single landmark reported in our previous study (Zhou & Mou, 2016). Two factors were determined. First, people might select multiple reference points from a circular boundary for multiple targets, one for each target. The larger number of reference points—multiple reference points from a circular boundary compared to one reference point from a single landmark—might therefore lead to less accurate cognitive mapping relative to a homogenous circular boundary than relative to a single landmark. Second, people might not encode the direct (straight line) relations among the multiple reference points in a homogenous circular boundary, although they may know that all of the reference points are on the same circular boundary.

Experiment 1 showed that more accurate representations of individual locations in the learning phase occur when participants use four wall segments (4OP_10) than when they must use one wall segment (1OP_10), but that, in the testing phase, equivalent accuracy in participants' knowledge of inter-location spatial relations emerges under both conditions. This result suggests that a larger number of reference points lead to less accurate cognitive mapping. Experiment 1 also showed that the cognitive maps derived in the whole wall condition (B) were less accurate than those derived in both the 1OP_10 and the 4OP_10 conditions. The contrast between the B condition and the 4OP_10 condition, in particular, suggests two possible factors that might have impeded cognitive mapping relative to the boundary, compared to cognitive mapping relative to four wall segments. First, participants might have selected more than four reference points in the whole wall condition. Second, participants might have selected four reference points from the whole wall but not encoded the direct relations among these four points. The results of Experiment 2 support the second possibility. Experiment 2 showed that when the extendedness of the wall segments increased, cognitive mapping performance remained stable, until the four wall segments were connected and became a continuous wall. When the four wall segments were separated, their direct relations were obvious and encoded. In contrast, participants in the continuous wall condition might not have encoded the direct relations among the four reference points, which led to less effective cognitive mapping. The findings of Experiment 2 also indicate that participants might have used four primary reference points (i.e., the optimal/closest wall segments) to encode the four targets. If they used more than four reference points, they would have been more likely to use a larger number of reference points when the extendedness of the wall segments increased; this would have led to less accurate cognitive mapping performance, which was inconsistent with the findings.

These findings support and extend the vector-addition model proposed by Zhou and Mou (2016). The vector-addition model stipulates that when multiple non-overlapping reference points are involved in encoding individual locations, the more complex addition process involved in inferring the spatial relations among the locations impairs cognitive mapping of inter-location spatial relations. One direct prediction of this model is that a larger number of reference points leads to less accurate cognitive mapping. The current study directly supports this prediction. Moreover, the finding that the direct spatial relations among the chosen reference points were not easily accessible to participants was also novel and consistent with the vector-addition model. According to the vector-addition model, in order to infer inter-location spatial relations, people need to know the spatial relations of the reference points for individual locations. Therefore, inferring inter-location spatial relations is easier when the spatial relations among the reference points are more accessible.

There are numerous findings in the reorientation geometry literature suggesting that humans and some other species prefer global geometry provided by an enclosed boundary in space over feature cues to reorient themselves (Cheng, 1986; Hermer & Spelke, 1994; for review, see Cheng & Newcombe, 2005). However, our findings suggest that such global information (all of the chosen reference points being on the same circle) did not help participants to incorporate representations of individual locations within a boundary into a cognitive map. Most importantly, when participants were locating a single object relative to a circular homogenous boundary, it appears that they broke down the global environment (segmenting the circular boundary) and attended more closely to the most relevant part of the environment so as to correctly encode the target location (e.g., choosing the optimal reference points). They were, however, less aware of the spatial relations between that particular part and the rest of the environment. Because the locations were sequentially learned and participants only attended to the local environment depending on the locations they were currently encoding, direct spatial links among the local parts were not formed; this impaired cognitive mapping relative to the boundary to a substantial extent. One possibility is that the knowledge of the global shape of the boundary would overshadow the process of encoding the direct spatial relations among the chosen four reference points, as participants were not explicitly motivated to learn the spatial relations among the chosen reference points (they were not told of the testing tasks beforehand).

In addition, Experiment 1 demonstrated that localization performance in the learning phase (involving representations of individual locations with the original localization cues) was less accurate in the whole-wall condition than in the four-segment condition. We hypothesized that localization relative to a homogenous circular boundary should be more challenging, as segmenting the boundary according to distal orientation cues consumes mental resources, whereas the segmentation process was spared when four separate wall segments were already available in the environment. To represent a particular location within the boundary (the localization process), participants needed to choose the most informative wall segments (in the case of localization, the segments of the whole boundary that were closest to a particular location) as the optimal/primary reference point for encoding the location. Although participants were able to segment the boundary and pick out the optimal or nearly optimal reference points for the four locations, this mental segmentation and selection process added to the work load involved in the localization task. Meanwhile in the 4OP_10 condition, the four optimal reference points were already identified in the environment, and participants just needed to assign the appropriate wall segments to the corresponding objects' locations as the reference points (i.e., identifying which object was close to which one of the four wall segments), and to establish vectors between the locations and the reference points. Hence localization relative to a homogenous circular boundary is more difficult, as the optimal/primary reference points need to be mentally segmented out and chosen, which leads to poorer representations of individual locations relative to the whole boundary than relative to the four separate wall segments.

The current study used a homogenous circular wall to investigate localization and the cognitive mapping process relative to a boundary. The use of such a boundary is likely to confine the generalizability of the current findings to situations involving boundaries of other shapes or boundaries with distinctive visual features on them. It is possible that boundaries of irregular shapes or boundaries with other visual features would already have distinctive segments available, which would consequently spare participants’ efforts in the initial segmentation process. As a result, participants might be able to detect and encode the direct spatial relations among different segments of the boundary; the process of cognitive mapping in this case might be improved relative to the case of a homogenous circular boundary. Confirmation of this speculation, however, would demonstrate again that a localization process within a bounded space does not necessarily engage the global structure of the space.

Following the current results of the study, we propose a two-stage localization process within a bounded space: first the boundary is segmented into sections and the sections are differentiated by an individual; second, to encode a specific location, the individual uses the most informative section of the boundary (e.g., the segment of the boundary closest to the location) as the reference point for the location. Thus, different locations have different sections as their respective reference points, and the locations are encoded within a fragment of the bounded space rather than relative to the whole space. Our study demonstrated that knowledge about the direct spatial relations among these separate fragments is not necessarily actively encoded.

3.6 References

Barry, C., Lever, C., Hayman, R., Hartley, T., Burton, S., O'Keefe, J., Jeffery, H., & Burgess, N. (2006). The boundary vector cell model of place cell firing and spatial memory. *Reviews in the Neurosciences*, *17*(1-2), 71-97.

Barry, C., & Burgess, N. (2007). Learning in a geometric model of place cell firing. *Hippocampus, 17*, 786-800.

Bennett, A. T. D. (1996). Do animal have cognitive maps. *The Journal of Experimental Biology*, *199*, 219-224.

Bird, C. M., Capponi, C., King, J. A., Doeller, C. R., & Burgess, N. (2010). Establishing the boundaries: the hippocampal contribution to imagining scenes. *The Journal of Neuroscience, 30*(35), 11688-11695.

Bohbot, V. D., Kaline, M., Stepankova, K., Spackova, N., Petrides, M., & Nadel, L. (1998). Spatial memory deficits in patients with lesions to the right hippocampus and to the right parahippocampal cortex. Neuropsychologia, *36*(11), 1217-1238.

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

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

Doeller, C. F., & Burgess, N. (2008). Distinct error-correcting and incidental learning of location relative to landmarks and boundaries. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(15), 5909-5914.

Doeller, C. F., King, J. A., & Burgess, N. (2008). Parallel striatal and hippocampal systems for landmarks and boundaries in spatial memory. *Proceedings of the National Academy of Sciences of the United States of Americ*a, *105*(15), 5915-5920.

Ekstrom, A. D., Kahana, M. J., Caplan, J. B., Fields, T. A., Isham, E. A., Newman, E. L., & Fried, I. (2003). Cellular networks underlying human spatial navigation. *Nature*, *425*, 184-188.

Gouteux, S., & Spelke, E. S. (2001). Children's use of geometry and landmarks to reorient in an open space. *Cognition, 81*, 119-148.

Hartley, T., Maguire, E. A., Spiers, H. J., & Burgess, N. (2003). The well-worn route and the path less traveled: Distinct neural bases of route following and wayfinding in humans. *Neuron*, *37*, 877-888.

Hartley, T., Burgess, N., Lever, C., Cacucci, F., & O'Keefe, J. (2000). Modeling place fields in terms of the cortical inputs to the hippocampus. *Hippocampus, 10*, 369-379.

Hartley, T., Trinkler, I., & Burgess, N. (2004). Geometric determinants of human spatial memory. *Cognition*, *94*(1), 39-75.

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

Iaria, G., Petrides, M., Dagher, A., Pike B., & Bohbot, V. D. (2003). Cognitive strategies dependent on the hippocampus and caudate nucleus in human navigation: Variability and change with practice. *The Journal of Neuroscience*, *23*(13), 5945-5952.

Levine, M., Jankovic, I. N., & Palij, M. (1982). Principles of spatial problem solving. *Journal of Experimental Pscyhology: General*, *111*(2), 157-175.

Marchette, S. A., Bakker, A., & Shelton, A. L. (2011). Cognitive mappers to creatures of habit: Differentail engagement of place and response learning mechanisms predicts human navigational behavior. *The Journal of Neuroscience*, *31*(43), 15264-15268.

McDonald, R. J., & White, N. M. (1994). Parallel information processing in the water maze: evidence for independent memory systems involving dorsal striatum and hippocampus. *Behavioral Neural Biology*, *61*(3), 260-270.

Mou, W., Nankoo, J., Zhou, R., & Spetch, M. L. (2013). Use of geometric properties of landmark arrays for reorientation relative to remote cities and local objects. *Journal of Experimental Psychology: Learning, Memory and Cognition, 40*(2), 476-491.

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), 1115-1127.

Nadel, L. (2013). Cognitive maps. In D. Waller & L. Nadel (Eds.), *Handbook of spatial cognition* (pp. 155-171). Washington, DC, US: American Psychological Association.

O’Keefe, J., & Dostrovsky, J. (1971). The hippocampus as a spatial map. Preliminary evidence from unit activity in the freely-moving rat. *Brain Research*, *34*, 171-175.

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

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

Zhou, R., & Mou, W. (2016). Superior cognitive mapping through single landmark-related learning than through boundary-related learning. *Journal of Experimental Psychology: Learning, Memory and Cognition*. In press.

Chapter 4

When boundary-related learning is not incidental: Perceived stability modulates cue-selection process in goal localization

4.1 Abstract

Two types of environmental visual cues have been identified as reference points used by individuals to encode locations: surface-based boundary cues and discrete-object-based landmark cues. Previous research has shown that learning locations relative to a boundary can overshadow learning relative to a landmark, but not vice versa, suggesting that boundary cues play a privileged role in representing individual locations (Doeller & Burgess, 2008). However, other research has revealed that a less accurate cognitive map is derived from the boundary than from the single landmark, suggesting that a boundary is a less privileged cue in representing inter-location spatial relations (Zhou & Mou, 2016). The current study aims to reconcile these inconsistent findings. Experiment 1, using both an overshadowing paradigm and a cognitive mapping task, replicated the finding that participants preferred a circular boundary to a four-landmark array for encoding four locations, but that the cognitive maps of the locations derived from the landmark array were more accurate. Using the overshadowing paradigm, Experiment 2 and 3 manipulated the relative stability and distinctiveness of the two cues. The results showed that increasing the stability of the landmark array decreased the overall cue preference for the boundary in encoding individual locations. We propose that the boundary privilege occurs in selecting reference points for encoding individual locations due to the salience of the boundary, whereas the landmark advantage occurs in inferring inter-location spatial relations due to the common reference point provided by the single landmark.

4.2 Introduction

Localizing oneself and other places of interest is important in our daily life. Successful navigation relies on accurate representations of individual location. Various cues from the physical environment (such as visual features in the surroundings) and during the course of navigation (such as the proprioceptive cues generated from locomotion through the environment) support the encodings and representations of individual locations. For the current study, we focused mainly on the visual features available in the environment. The localization literature has identified two types of environmental visual cues that can serve as reference points for encoding locations (Burgess, 2008; Lew, 2011), mainly surface-based boundary cues (e.g., walls, rivers) or discrete-object-based landmark cues (e.g., buildings, trees).

Differences in the processing of the two cues in a localization task were initially found in lesion studies on rats using Morris Water Maze (MWM) tasks (Morris, 1981). In one typical setup, rats are trained to swim to a submerged platform in a circular water tank filled with opaque water (escaping from the water is a strong motivator for rats to find the platform). Distal visual features are provided outside the water tank so that rats can keep oriented but these orientation cues cannot offer the exact location information of the platform. Instead the platform location can be specified relative to the boundary of the tank (i.e., in certain distance away from a part of the wall, e.g., Morris, 1981; Hamilton, Akers, Weisend & Sutherland, 2007) or relative to an intramaze landmark (i.e., bearing a certain spatial relation relative to an intramze landmark, e.g., Pearce, Roberts & Good, 1998). Several studies showed that hippocampal lesion in rats resulted in failure of finding the submerged platform when the platform location was fixed in the circular water tank however the lesion did not prevent rats from using a beacon cue (e.g., a visible feature attached to the platform) to find the platform (Morris, 1982; Packard & McGaugh, 1992; McDonald & White, 1994). Moreover such lesion did not impair rats finding a platform that had a fixed spatial vector relative to a landmark even though the landmark moved within the water maze across trials (Pearce, Roberts & Good, 1998). Given these findings, it has been proposed that learning locations in relation to the extramaze distal cues and the boundary is form of place learning and the process relies on hippocampus, whereas learning locations relative to the intramaze landmark might be hippocampal-independent (Burgess, 2008; see also Bullens et al., 2010).

The proposal that boundary processing in spatial localization relies on hippocampal activities is further supported by the findings of places cell within rats hippocampus (O'Keefe & Dostrovsky, 1971; O'Keefe, 1976; see also Burgess, 2008); the firing of these cells corresponds to the locations of a rat in a given environment. Since the initial discovery of place cells, several models have been put forward to explain how they code spatial information (for review, see Redish, 1999). One of the influential models proposed by O'Keefe and Burges (1996) postulates that environmental boundaries act as a major input to drive the spatial-specific firings of the hippocampal place cells, based on their finding that a given place cell would reach its peak firing when the rat (moving in a rectangular or square enclosure) was at a fixed distance to an enclosure wall in a fixed allocentric direction (the reference system define by the main axes of the enclosure). A later modified version of the model, the Boundary Vector Cell (BVC) model, suggested that individual place cells received a summation of inputs from an ensemble of boundary vector cells (BVCs) whose firings were thought to be tuned to a barrier or a boundary at a given distance and allocentric direction from a rat (Hartley et al., 2000; Harley, Trinkler & Burgess, 2004; Barry et al., 2006; Burgess, 2008). The existence of the hypothetical BVCs was also confirmed in the subiculum of rats (Lever et al., 2009). Contrary to the finding that environmental boundary information exerts control over the firing of place cells and hippocampal activities, landmark arrays placed in the center of a cylinder arena were shown to exert little control over the firing field of place cells (Cressant, Muller & Poucet, 1997).

Apart from the models and single-neuron recording studies on rats, neruoimaging studies on human participants have given corroborating evidence that boundaries, rather than discrete local landmarks, are a major input driving human hippocampal activities. Using functional MRI to examine the neural bases of participants localizing four objects in a computerized version of the Morris Water Maze (MWM) task, Doeller, King and Burgess (2008) found that encoding locations relative to a circular boundary corresponded to the neural activation in hippocampus; meanwhile, encoding locations relative to a single landmark within the boundary was associated with the activation in the dorsal striatal area. Another fMRI study demonstrated that imagining horizontal boundaries rather than vertical columns was associated with hippocampal activities (Bird, Capponi, King, Doeller & Burgess, 2010).

The differing effects of the boundary cue and the landmark cue on behavioral localization tasks are also observed in human participants (Doeller & Burgess, 2008). Using a cue-competition paradigm (shadowing and blocking), Doeller and Burgess adapted the MWM tasks in a desktop virtual-reality environment. In their overshadowing experiment, participants learned to place four objects relative to a featureless circular wall (the boundary condition), a single traffic cone (the landmark condition, the landmark was placed within the radius of the boundary) or with the presence of both cues (the two compound-cue conditions). Distal orientation cues were provided in all the conditions and participants had to rely on the respective localization cues to accurately encode the four objects' locations. During the subsequent testing phase, participants in the boundary and the landmark conditions were tested with the presence of their respective localization cues, without feedback, meanwhile those in the compound-cue conditions were tested with one of the two cues removed. Localization performance was measured as the distance between the response locations (where participants placed the objects) and the corresponding correct locations.

The results revealed that participants in the compound-cue condition who were later tested with the landmark alone (i.e., with the boundary removed) were less accurate in locating the objects during the testing phase compared to those in the landmark condition (in which the traffic cone was presented in both the learning and the testing phase). Such inferior test performance was not observed in the compound-cue group who were tested with the boundary alone (i.e., with the landmark removed) in comparison to the boundary group (in which the boundary was presented in both the learning and the testing phase). Thus, learning locations relative to the boundary overshadowed learning locations to the single landmark when both cues were available in the environment (participants, however, were able to use the landmark as a localization cue when the landmark was the only cue available, as shown in the landmark condition). The authors suggested that boundary-related learning is incidental and governed by place learning mechanisms, whereas landmark-related learning obeys the rules of associative learning. Hence, according to the authors, the boundary advantage in encoding locations might be a result of the different learning mechanisms underlying the spatial learning relative to the two cues.

In addition to gaining accurate representations of individual locations, in order to successfully navigate in a large environment that is beyond one’s vicinity, one has to integrate separate spatial memories (e.g., representations of individual locations) acquired at different points in time, and in different spaces, into a unified representation of the environment, much like combining pieces of puzzles to make a whole picture. For example, knowing where one's office and the grocery store are spatially situated in relation to one's home will enable a successful trip between the office and the grocery store, even though one might never travel directly between the two locations before. Such integrated representations, which allow for the inference of spatial relations between two locations (i.e., a vector between two locations that specifies direction and distance information), are called *cognitive maps* (Tolman, 1948; see also Nadel, 2013; Bennet, 1996). We refer to this integration process as *cognitive mapping*.

Although surface boundaries as a localization cue have been assigned a privileged role over object-based landmarks in encoding individual locations (it is thought, for example, that there is a lack of cue competition from landmark cues over boundary cues in goal localization), less is known regarding their roles in the cognitive mapping process. The study in Chapter 2 (see also Zhou & Mou, 2016) used both a novel-vector inference task (Experiment 1) and a configuration judgement task (Experiment 2) to assess the qualities of the cognitive maps derived from either a circular featureless boundary cue or a single landmark cue. Participants learned sequentially the locations of four objects in an immersive virtual-reality environment with either a circular wall (the boundary condition) or a traffic cone which was placed within the range of the boundary (the landmark condition). In addition to the localization cues, distal orientation cues were provided in both conditions. In the subsequent testing phase, the original localization cues were removed (the wall in the boundary condition and the traffic cone in the landmark condition). Instead one of the four objects (Experiment 1) or two of the four objects was/were shown at its/their correct locations as the localization cues and participants were asked to place the remaining objects back while the distal orientation cues were kept. The tasks directly examined the relative quality of the cognitive maps derived from the learning phase with respective localization cues.

The results revealed a less accurate map (in terms of inferior inferences of novel spatial vectors between two locations and inferior configuration judgment among three locations) of the four locations derived from the boundary than from the single landmark. Note that individual representations of the four locations acquired from the two cues were comparable (as revealed by participants' equivalent accuracy in locating the four objects relative to either cue at the end of the learning phase). Thus, the inferior cognitive maps developed from the boundary-related spatial learning seem to be resulted from the differences in the cognitive mapping processes relative to the two cues.

To explain such single-landmark advantage in cognitive mapping (more accurate cognitive maps derived from the landmark cue), Zhou and Mou (2016) proposed a vector addition model. The model posits that regardless of the underlying mechanisms, in order to successfully represent a location, a vector needs to be established between the location and a chosen reference point from the environment. When two locations are encoded relative to a common reference point (such as the single traffic cone), cognitive mapping is relatively simple, as one only needs to add the two individual vectors (each vector encodes the spatial relation between the common reference point and one of the two locations) together to infer the third vector between the two locations. However when two locations are encoded relative to two distinctive reference points (one reference point per location), cognitive mapping is relatively more difficult as one also needs to encode the spatial relation between the two chosen reference points and add this vector into the aforementioned addition process. The boundary cue (such as the circular wall) provides multiple reference points for encoding different locations within the enclosure (see also Mou & Zhou, 2013), leading to a more complex vector addition process during cognitive mapping.

The finding that a single landmark, rather than a boundary, was a more effective cue in cognitive mapping is surprising, given previous findings suggesting the superiority of the boundary over the single landmark (Doeller & Burgess, 2008; Mou & Zhou, 2013). Furthermore, given the important role of hippocampus rather than the striatal system in forming cognitive maps (O'Keefe & Nadel, 1978; Iaria, Petrides, Dagher, Pike, & Bohbot, 2003; Ekstrom, et al., 2003; Hartley, Maguire, Spiers, & Burgess, 2003; Marchette, Bakker, & Shelton, 2011) and the control of boundaries on hippocampal activities, one would expect a more accurate cognitive map to be developed from the boundary cue.

The major goal of the current study is to reconcile the inconsistent findings regarding the different advantages of a boundary cue and a landmark cue depending on the spatial tasks involved (Doeller & Burgess, 2008; Zhou & Mou, 2016). We hypothesize that encoding individual locations and inferring spatial relations among locations are two separate stages. The advantage of a boundary cue occurs in the former stage whereas the advantage of a single landmark occurs in the latter stage. The advantage of a boundary cue in encoding individual spatial locations might result from the perception that it provides "better" reference points during the initial stage of goal localization. Upon first encountering an environment, with a navigational goal in mind (e.g., to remember a certain location of interest), people evaluate the usefulness of different features provided in the environment in order to choose an appropriate cue to achieve their goal. Different weightings are then assigned to different environmental features depending on their evaluated usefulness, which determines the relative reliance upon a particular cue. In the case of encoding a particular location, it is likely that a stable, distinctive feature of the environment would be favored as the reference point for the location. We refer to this process as reference-point selection. We propose that two physical features of a boundary cue could potentially give rise to its advantageous role in cue competition with a landmark cue.

First, a boundary cue surrounding a navigator might be perceived more stable in comparison to a single intramaze landmark. Evidence from reorientation literature suggests that perceived cue validity, such as the perceived stability of an environmental cue, affects the degree of reliance on a particular environmental cue used in navigation (Newcombe & Ratliff, 2007). Single-neuron recording studies have shown that a less stable visual cue used as an orientation cue has weaker control over the place field and the head direction cell firings (Knierim, Kudrimoti & McNaughton, 1995; Jeffrey, 1998). Therefore a boundary cue perceived as a more stable environmental feature would exert more control on a spatial behavior in comparison to a single landmark.

Second, a boundary cue based on continuous surface could provide multiple distinctive reference points for encoding individual locations within the boundary. In our previous work, we proposed a possible localization process relative to a circular boundary together with distal orientation cues (Mou & Zhou, 2013; see also Zhou & Mou, 2016). For instance, when participants were localizing within the circular wall (Figure 4.1), using the distal orientation cues allowed them to segment the continuous surface into different wall segments (e.g., the segment closest to the north). Participants could then use an appropriate wall segment (i.e., the wall segment closest to a target location compared to all the other segments) as the optimal reference point for a particular target location (e.g., the candle referred to be five meters south of the North wall). Thus, each target location within the boundary could be associated with a unique reference point (a wall segment distinguished by an aligning distal orientation cue). By contrast, a single landmark could only serve as a common reference point for encoding a set of locations, which would cause potential interference in location representation and retrieval. This postulate is inspired by the interference theory in associative learning and memory literature (for a brief review see Anderson, 2003) which proposed that forgetting can be induced by adding new memory trace to an old retrieval cue. Hence a single landmark would be evaluated as a less useful cue for encoding a set of individual locations than a boundary that provided distinctive reference points. Consequently, in order to ensure that representations of individual locations would be unique from each other (thus less interference), distinctive environmental cues would be favored.

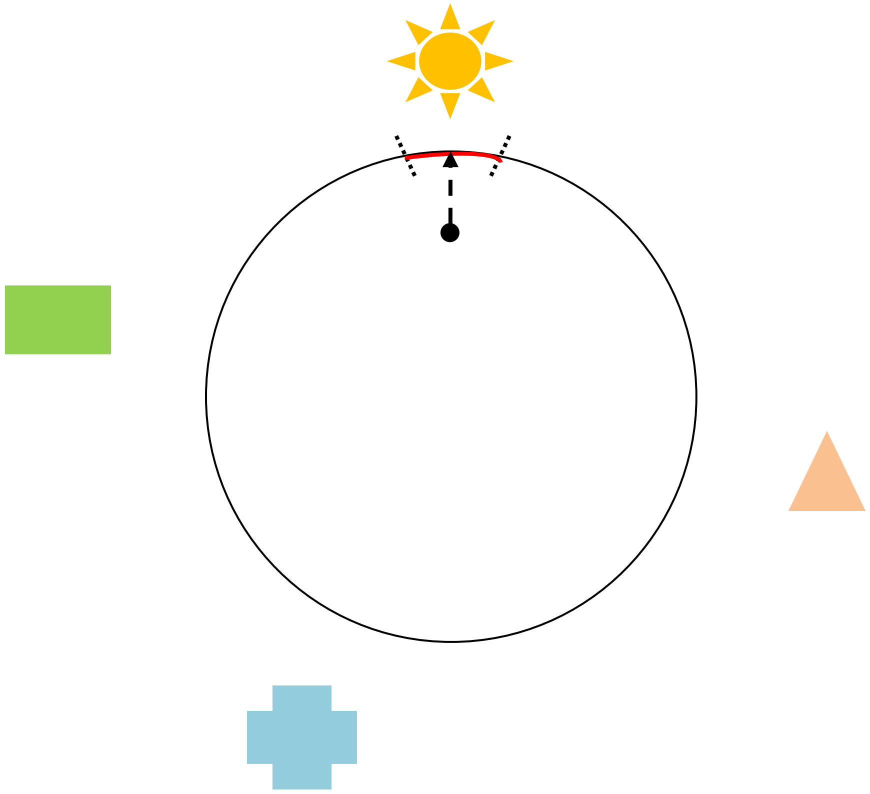


Figure 4.1. Schematic illustrations of encoding a single location relative to a circular homogeneous boundary. The target location is illustrated as the dot within the circle. The four shapes illustrated distal orientation cues. The two dashed lines illustrated segmentation based on

the distal orientation cues and the red wall segment chosen as the optimal reference point for encoding the target location. The dotted arrow illustrates the vector established between the location and the chosen wall segment.

Three Experiments were employed to test the potential contributions of the aforementioned factors in modulating the relative degree of reliance upon a boundary cue and landmark cue in encoding individual locations. In a single experiment, Experiment 1 replicated the previous findings regarding the superiority of a boundary over four landmarks in encoding individual locations, and the superiority of four landmarks over the boundary in cognitive mapping. One group of participants were employed in an overshadowing paradigm (similar to Doeller & Burgess 2008, see also Mou & Zhou, 2013) to assess cue competition between a circular wall (the boundary) and an intramaze landmark array, consisting of four identical traffic cones, in the process of encoding four locations. The other group of participants were employed in a novel-vector inference task (similar to Experiment 1 in Zhou & Mou, 2016) to assess the relative accuracy of the cognitive map derived from the circular wall vs. that derived from the four-cone array. In Experiments 2 and 3, using the same overshadowing paradigm, we manipulated the relative stability and the distinctiveness of the landmark array to examine whether and how the two factors modulate the degree of reliance upon the two cues during the cue-selection process.

4.3 Experiment 1

Two spatial tasks were employed to assess the relative advantages of a boundary cue and a landmark cue in encoding individual locations and in cognitive mapping. The superiority of a landmark in cognitive mapping and the superiority of a boundary in cognitive mapping had previously been reported in separate studies varying in many uncontrolled variables. By using a single experiment in the current study, we assured that the relative advantages of a boundary cue and a landmark cue in encoding individual locations and in cognitive mapping were caused specifically by the different tasks, rather than by other uncontrolled variables. Furthermore, we used four landmarks instead of one landmark in the current experiment. Each landmark was intentionally paired with one of the four target locations so that the distance between one landmark and its corresponding target location was the same as the shortest distance between that particular location and the boundary (for detailed illustrations see Figure 2). In this way, we eliminated the differences between the circular wall and the four-landmark array in terms of their distance to the four targets and the number of reference points.

One group of participants (referred to as the Doeller & Burgess' task group) learned the locations of four objects sequentially, in the presence of both a circular wall (the boundary) and a cone array consisting of four identical traffic cones (the landmark). In the subsequent testing phase, one of the two cues (the circular wall or the cone array) was removed and participants were asked to replace the four objects based on the remaining cue. Relative accuracy of the localization performance during testing compared to that during learning was thought to reflect the degree of reliance upon the remaining cues.

The other group of participants (referred to as the Zhou & Mou's task group) learned the locations of four objects sequentially, using as a localization cue either the circular wall (the boundary condition) or the cone array (the landmark condition). During the subsequent testing phase, participants were asked to infer the spatial relations between two of the four locations based on their representation of the individual locations. Localization performance during testing was thought to reflect the quality of cognitive maps derived from the respective learning cues.

4.3.1 Method

Participants. Ninety-six (48 males and 48 females) students from the University of Alberta participated to fulfill a course requirement. Among them, 48 participants (24 males and 24 females) participated in the Doeller & Burgess' task and the other half (24 males and 24 females) in the Zhou & Mou's task. A criterion was set before the study that participant with a mean response errors larger than 100 virtual meters (vm) would be excluded (the boundary was 50 vm in radius).

Materials and Design. In the Doeller & Burgess' task group, an immersive virtual environment was displayed using an nVisor SX60 head-mounted display (HMD) (NVIS Inc., Virginia). Graphics were rendered using the Vizard software (WorldViz, Santa Barbara, California). Head orientation was tracked with an InterSense IS-900 motion tracking system (InterSense Inc., Massachusetts). Thus, through head rotation, participants could change their viewpoints. Participants used a joystick to translate, to pick up and to place back the objects in the virtual environment.

In the virtual environment (Figure 4.2A), participants learned four locations on infinite grassland by picking up four sequentially presented objects (a candle, a lock, a bottle and a wood block) and then placing them at the correct locations. A fixed set of locations was used for all the participants; however, the object-location pair was randomized across participants. During the learning phase, both a visually homogeneous, circular wall (the boundary cue) and a cone array consisting of four identical traffic cones (the landmark cue; each traffic cone was visually homogeneous as well, illustrated as the triangles in Figure 4.2A) were presented as the localization cues. Four different scenes (Ocean, Forest, Mountain and City) were set at an infinite distance from participants as distal orientation cues (indicated by the surrounding labels in Figure 4.2). In the testing phase (Figure 4.2B), for half of the participants, the circular wall was removed and the participants were asked to place the objects to their correct locations based on the remaining cone array and the distal orientation cues (the condition is referred to as LB-L). For the remaining half of the participants (Figure 4.2C), the cone array was removed during testing, and the participants were asked to replace objects based on the remaining circular wall and the distal orientation cues (this condition is referred to as LB-B).

Each traffic cone in the cone array was (unknown to the participants) intentionally paired with one of the four locations so that the distance between one cone and its corresponding target location was the same as the shortest distance between this particular location and the circular wall (for detailed illustrations see Figure 4.2). In addition, each traffic cone was also intentionally placed as far inwards from the circular wall as possible while still maintaining a distance from the other three unpaired locations. Hence the overall distance between the landmark array and the four locations was smaller than the overall shortest distance between the wall and the four locations, which increased the relative reliability of the landmark cue as the potential reference points for the four locations. Previous research has demonstrated that a landmark closer to a target location has more control as a reference point than a further-away landmark in encoding the particular location (Cheng, 1989; Spetch, 1995). One question we were also interested in was whether this increased reliability in the landmark cue could modulate the relative weightings assigned to the two cues, leading to an increased reliance upon the landmark cue. That is, we sought to determine whether we would see some overshadowing effect from the landmark cue over the boundary cue, if increasing the reliability of the landmark cue, by positioning the cone array closer to the four locations, made the landmark array a more “competitive” set of reference points for encoding the four locations.

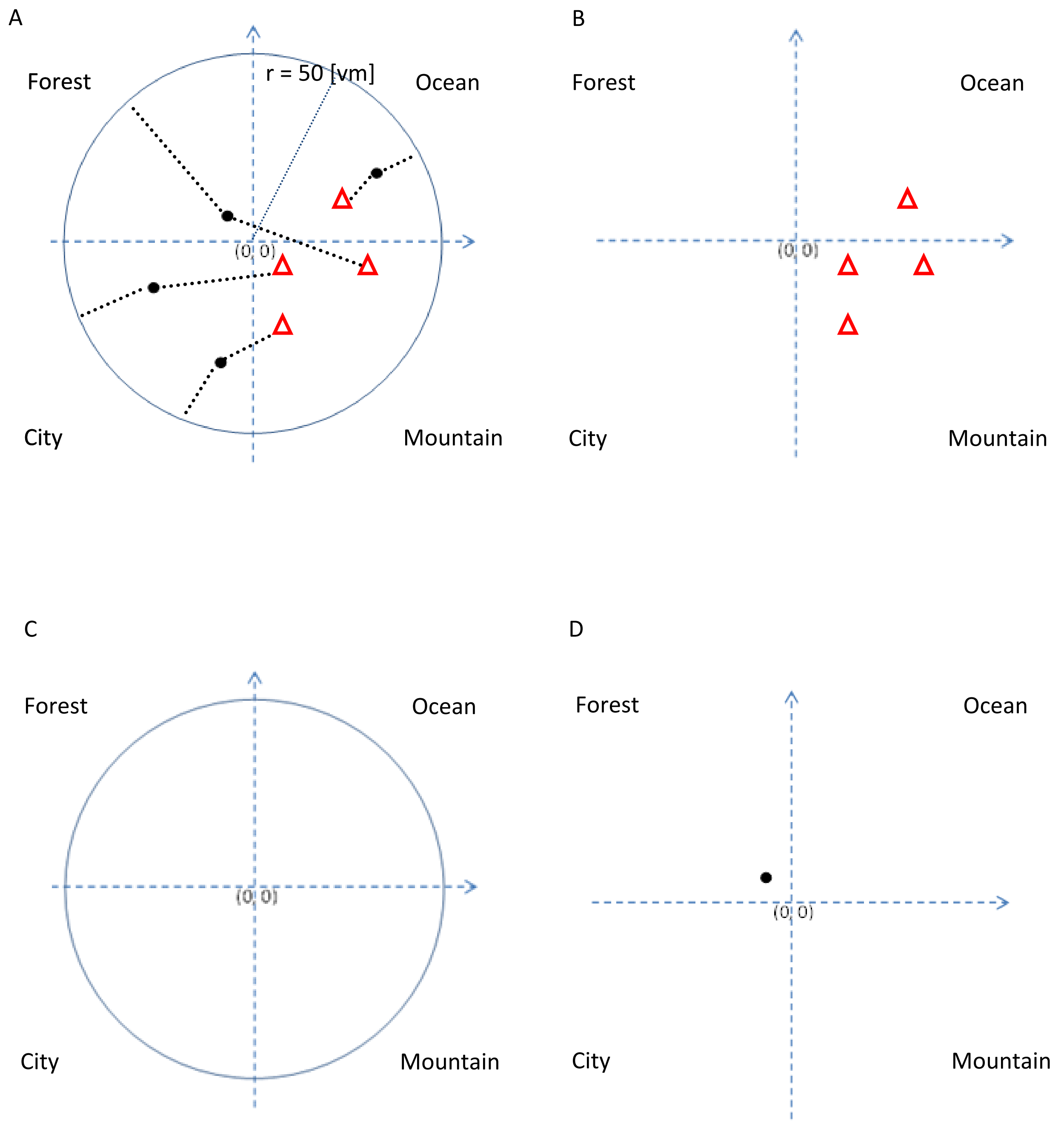


Figure 4.2. Top-view illustrations of the virtual environments used in Experiment 1. A, The learning phase of the Doeller & Burgess' task group. The circle illustrates the wall, 50 virtual meters (vms) in radius which is also illustrated as the dashed line in the circle. The two dotted lines with arrows illustrate the coordinate axes where (0, 0) is the origin of the coordinate system

(and the center of the wall) used in the virtual-reality environment. The axes and the center are marked only for readers. The four dots illustrate the target locations. The coordinates of the four locations are (35.86, 19.88), (-7.74, -31.05), (-5.14, 6.13), (-18.02, -12.62) (units in vms). The four labels (Ocean, Mountain, City, and Forest) illustrate the background scenes set at an infinite distance from the center of the environment. The four-cone array is illustrated as the four red triangles. The dotted lines reveal that the shortest distance from each of the four locations to the circular wall is equivalent to one of the traffic cones paired with the particular location (these dotted lines were not marked in the experiment and participants were not aware of the pairings). The coordinates of the four traffic cones are (25.96, 13.08), (7.69, -21.78), (34.32, -8.24), and (8.29, -3.04); B, The testing phase of LB-L (the circular wall removed) in the Doeller & Burgess' task group in Experiment 1 as well as the learning phase of L in the Zhou & Mou's task group in Experiment 1; C, The testing phase of LB-B in the Doeller & Burgess' task group in Experiment 1 as well as the learning phase of B in the Zhou & Mou's task group in Experiment 1; D, The testing phase of both conditions (B and L) in the Zhou & Mou's task group in Experiment 1. The dot illustrates one of the four objects at its original location used as the testing cue for one particular trial. The original localization cue (the landmark or the boundary) was removed.

The experimental setup used in the Zhou & Mou's task group was mostly similar to that in the Doeller & Burgess' task group, with the following exception. Participants were randomly assigned to two conditions which differed in terms of the localization cue presented during the learning phase. One group of participants (Figure 4.2C) learned the four locations relative to the circular wall (the same wall used in the Doeller & Burgess' task group), together with the distal orientation cues. We referred to this condition as B. The other group (Figure 4.2B) learned the four locations relative to the four-cone array (the same traffic-cone array used in the Doeller & Burgess' task group), together with the distal orientation cues. We referred to this condition as L.

During the testing phase of the Zhou & Mou's task group (Figure 4.2D), the wall in B and the cone array in L were removed. However, one of the four objects was presented in each trial as the localization cue, together with the distal orientation cues. Participants needed to replace the other three objects. Because participants never saw the four objects simultaneously, the vectors between the cue objects and the probed objects had to be a product of cognitive mapping. Therefore, participants' testing performances in L or B could reflect the relative accuracy of cognitive mapping in each condition.

Procedure. In the Doeller & Burgess' task group, participants donned the HMD and sat on a swivel chair at the center of the experiment room. Each participant went through three phases: the pick-up phase, the learning phase and the testing phase. During the pick-up phase, participants collected the four objects one by one from the objects' original locations. The learning phase comprised four blocks of four learning trials (one trial per object in each block). During each learning trial, one of the four objects was probed, and participants replaced the probed object using their memory of its original location. After the response, the probed object appeared at its correct location. Participants were asked to collect it (this served as feedback allowing participants to learn the locations in a trial-and-error fashion). Participants' starting locations (could be anywhere within a range of 40 virtual meters from the center of the wall) and facing directions at the beginning of each trial were randomized. During the testing phase, the circular wall in LB-L and the cone array in LB-B were removed; the orientation cues, however, remained. With the exception of the removal of cues according to the conditions, the testing phase was conducted in exactly the same way as the learning phase. Participants replaced each of the four objects once in each block (thus four trials per block), over a total of four blocks. No feedback was given in the testing phase.

The procedure of the testing phase in the Zhou & Mou's task group was mostly similar to that in the Doeller & Burgess' task group, with the following exception. During testing, the wall in B and the cone array in L were removed. During each testing trial, one of the four objects was shown at its correct location as a localization cue together with the distal orientation cues; participants replaced one of the other three objects. The testing phase comprised four blocks of three testing trials. In each block, one of the four objects served as the testing cue in all three trials, and each of the other three objects was probed once.

4.3.2 Results

Response errors, measured as the distances between participants' response locations and the corresponding correct locations, were recorded as the dependent variable for all of the experiments in the study.

The Doeller & Burgess' task group. We analyzed the overshadowing effect by comparing the response errors of each participant in the testing phase with the response errors of the same participant in the learning phase. Increased response errors in the testing phase compared to those in the learning phase would indicate an impairment effect resulting from the removal of one of the two cues, which would be equivalent to a typical overshadowing effect. We were also interested in the relative degree to which such an effect would result from the removal of either of the two cues, if we did observe increased response errors during testing in both LB-B and LB-

L. As noted above, the particular arrangement of the cone array in the current experiment might increase the reliability of the landmark array compared to that of the landmarks used in the previous experiment (e.g., Doeller & Burgess, 2008; Mou & Zhou, 2013), which might lead to an impairment effect resulting from the removal of the cone array in LB-B. If a bi-directional overshadowing effect was observed, the relative degree of the two impairment effects (i.e., whether the increase in response errors in LB-L was larger than that in LB-B) might indicate the relative weightings assigned to the two cues.

Across the four learning blocks, there was a significant learning effect through feedback, F (3, 138) = 12.65, $p < .001$, $\eta_p^2 = .22$. Across the four testing blocks, however, there was no learning effect, F (3, 138) = .27, $p = .85$, $\eta_p^2 = .006$. This was expected, as no feedback was provided in the testing blocks. Similar results were observed in the subsequent experiments. Hence, only the response error in the last learning block was compared to the response error in the four testing blocks in this experiment and in Experiments 2 and 3. The mean response errors were averaged in the last learning block and in the four testing blocks for each participant.

The mean response errors are plotted as a function of condition (LB-L vs. LB-B) and experimental phase (last learning block vs. all testing blocks) in Figure 3. The mixed-model ANOVAs were conducted to analyze the impairment effect from removing different cues, with condition (LB-L vs. LB-B) as a between-subject variable and experimental phase (the 4th learning block vs all testing blocks) as a within-subject variable. An interaction between condition and experimental phase was revealed, F (1, 46) = 6.52, $p = .014$, $\eta_p^2 = .12$, as well as a main effect of experimental phase, F (1, 46) = 19.54, $p < .001$, $\eta_p^2 = .30$. The main effect of condition was not significant, F (1, 46) = 1.33, $p = .26$, $\eta_p^2 = .03$. Planned comparisons indicated that response errors increased significantly during the testing phase in LB-L, *t* (23) = 4.93, *p* < .001, Cohen's *d* = 1.42 ($M_{4th\_learning\ block}$ = 16.44 vm, $SD_{4th\_learning\ block}$ = 6.84; $M_{testing\_average}$ = 28.10 vm, $SD_{testing\_average}$ = 14.86), whereas the response errors during the testing phase in LB-B did not differ significantly from those during the last learning block, *t* (23) = 1.32, *p* = .2, Cohen's *d* = 0.38 ($M_{4th\_learning\ block}$ = 18.10 vm, $SD_{4th\_learning\ block}$ = 8.76; $M_{testing\_average}$ = 21.22 vm, $SD_{testing\_average}$ = 6.00)

These results indicated that the boundary cue overshadowed the landmark array in encoding individual locations. Even though in the current setup, the relative reliability of the landmark cue was increased (as the four optimal landmarks were used), a boundary advantage in encoding individual locations were still observed.

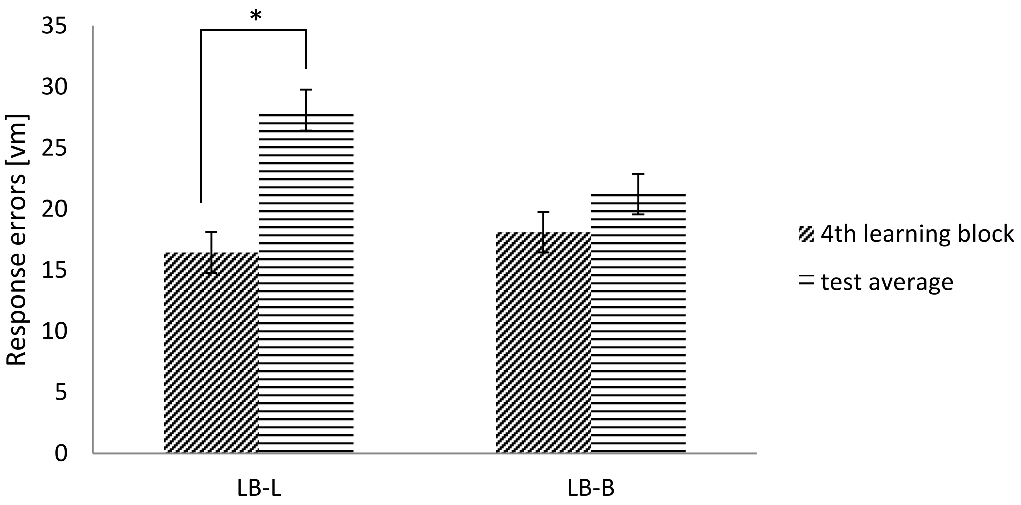


Figure 4.3. Response errors as a function of condition (LB-L or LB-B) and experimental phase (the fourth learning block or the average of all the testing blocks in the testing phase) in the Doeller & Burgess' task group in Experiment 1. Error bars are ± 1 standard error.

The Zhou & Mou's task group. The mean response error during the last learning block and the mean response error during the testing phase were examined separately, as we were interested in the relative quality of the cognitive maps derived from the respective learning cues between the two conditions.

The mean response errors of the last learning block were plotted as a function of learning-cue condition (L vs. B) in Figure 4.4. To ensure that participants in the two conditions acquired comparable representations of individual locations from respective localization cues after the learning phase, a one-way ANOVA was conducted on the mean response errors of the last learning block, with learning-cue condition as the between-subject variable. Participants in the two groups did not differ in terms of their localization accuracy at the end of the learning phase, $F\,(1, 46) = .0002$, $p = .99$, $\eta_p^2 < .001$ ($M_{\text{L-learning}} = 20.17$ vm, $SD_{\text{L-learning}} = 11.20$; $M_{\text{B-learning}} = 20.21$ vm, $SD_{\text{B-learning}} = 8.36$, units in virtual meters [vm]). Thus, representations of individual locations in the two conditions were comparable.

The mean response errors across four testing blocks were plotted as a function of learning-cue condition (L vs. B) in Figure 4.4. A one-way ANOVA was conducted to examine the relative quality of cognitive maps derived from the two conditions. A main effect of learning-cue condition was revealed, $F\,(1, 46) = 6.59$, $p = .01$, $\eta_p^2 = .13$ ($M_{\text{L-testing}} = 33.40$ vm, $SD_{\text{L-testing}} = 11.14$; $M_{\text{B-testing}} = 47.63$ vm, $SD_{\text{B-testing}} = 24.76$). Thus, participants who learned the locations relative to the landmark array developed a more accurate cognitive map, in terms of inferring spatial relations between two locations, than those who learned relative to the boundary.

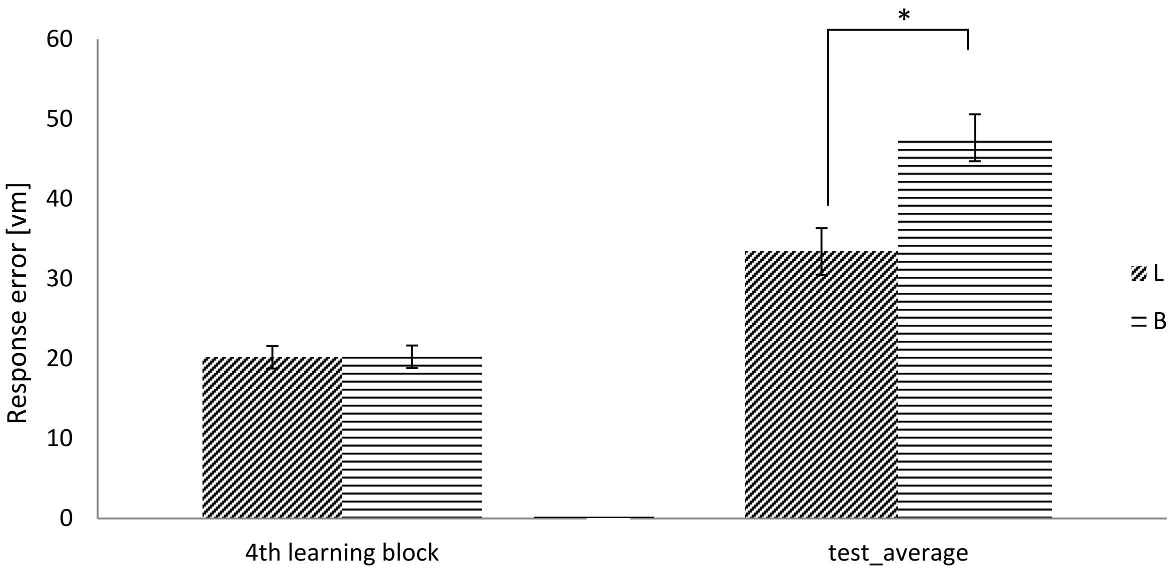


Figure 4.4. Response errors during the fourth learning blocks and response errors during the testing phase, as a function of learning-cue condition (L or B) in the Zhou & Mou's task group in Experiment 1. Error bars are ± 1 standard error.

4.3.3 Discussion

Experiment 1 replicated previous findings, demonstrating a boundary advantage over the four-landmark array in encoding and representing individual locations, as well as an advantage in using the landmark cue for the cognitive mapping of novel spatial relations. Note that the boundary advantage does not correspond to a higher accuracy of localization relative to the boundary cue, as the results of the Zhou & Mou's task group clearly indicated that the representations of individual locations acquired from either of the two cues were equally accurate. The advantage of the landmark cue over the boundary cue in cognitive mapping was still prominent even though the cone array also provided multiple reference points (one for each target location) for encoding individual locations.

We hypothesize that the boundary advantage might have been prominent during the reference-point selection process at the initial stage of goal localization in the Doeller & Burgess' task group. By contrast, participants in the Zhou & Mou's task group only saw one type of cue, so they did not engage in the reference-point selection process. The representations of individual locations acquired from the landmark array were as accurate as those acquired from the boundary.

The preference for the boundary cue during the reference-point selection process at the initial stage of goal localization might be due to the perceived physical characteristics of the boundary, which was further tested in the following experiment.

4.4 Experiment 2

As we proposed in the Introduction, the perceived higher stability of a boundary cue and the distinctiveness of the multiple reference points provided by the boundary could be key factors modulating the preference for the boundary cue over a landmark cue (i.e., more weightings/reliance are assigned to the boundary when participants are selecting reference points for encoding locations). In Experiment 2, we increased the relative stability and distinctiveness of the landmark array by moving each of the traffic cones in the cone array outwards and closer to the boundary. We did so in an effort to increase the perceived stability of the cone array, as well as make each cone more distinguishable from each other in terms of further distances.

Participants learned the locations of four objects with the presence of both a circular wall (as that in Experiment 1) and a landmark array consisting of four identical traffic cones placed outwards (Figure 4.5A). During the testing phase, one of the two cues was removed.

Representations of individual locations were tested with the remaining cue depending on the conditions.

4.4.1 Method

Participants. Forty-eight (24 males and 24 females) students from the University of Alberta participated to fulfill a course requirement.

Materials, Design, and Procedure

The materials, design, and procedure were similar to those employed in the Doeller & Burgess' task group in Experiment 1, except that each of the four traffic cones was moved towards the circular wall while the distance between each cone and its corresponding target location was mainted (see triangles in Figure 4.5A). Thus, for each target location, there would be one optimal reference point available from the circular wall (the point closest to a particular target location from all the points on the wall) as well as from one of the four traffic cones with equal distance. The group that was tested with the boundary alone was referred to as OLB-B (OL standing for *Optimal Landmark*) and the group tested with the landmark array alone was referred to as OLB-OL (Figure 4.5B).

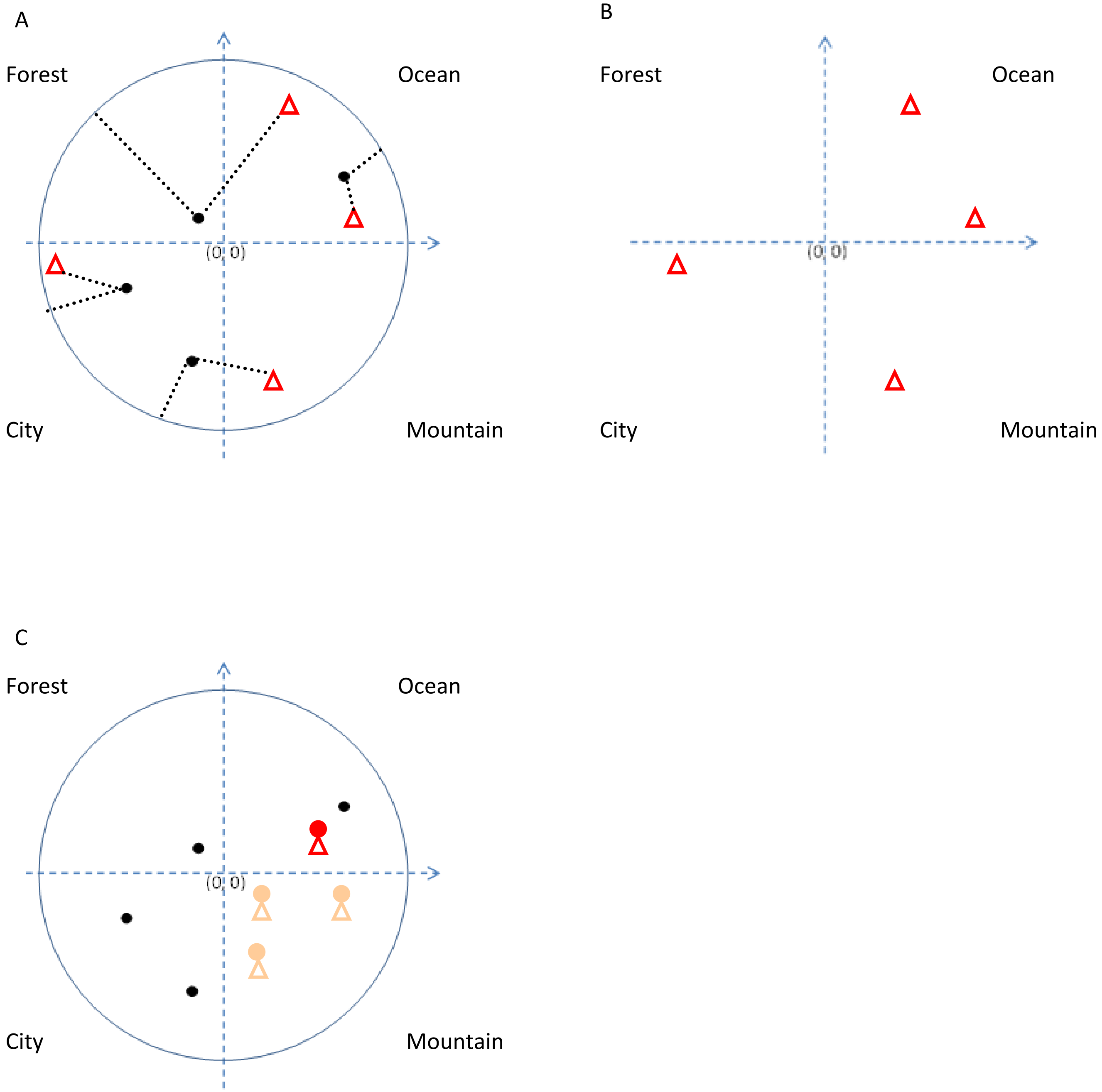


Figure 4.5. Top-view illustrations of the virtual environments used in Experiment 2 and 3. A, The learning phase of Experiment 2. The four traffic cones (the same as those used in Experiment 1) were placed further outwards and closer to the wall than those in Experiment 1. Each traffic cone was kept at the same distance from its paired target location, which was the

shortest distance from the particular target location to the wall. The coordinates of the four traffic cones were (37.27, 10.99), (9.72, -35.40), (27.03, 33.13), and (-45.60, -7.76), respectively; B, The testing phase of LB-L (with the circular wall removed) in Experiment 2; C, The learning phase in Experiment 3. The circular wall as well as one of the four traffic cones was presented at a particular learning trial. The identity of the presented traffic cone varied across trials, depending on the target location that was to be learned in a particular trial. In this particular trial, the traffic cone presented to participants was located at (25.96, 13.08). The red dot illustrates the small object model (the candle, the bottle, the lock or the wood) attached to the top of the traffic cones, the function of which was to increase the distinctiveness of each traffic cone. For the purpose of illustration, the other three traffic cones and their corresponding objects were also depicted, though they were not seen by participants at this particular trial. The light-red triangles illustrated the other not-presented three traffic cones, which were located at (7.69, -21.78), (34.32, -8.24), and (8.29, -3.04) respectively. The light-red dots represent the three model objects attached to the top of the three traffic cones.

4.4.2 Results and Discussion

The mean response errors are plotted as a function of condition (OLB-B vs. OLB-OL) and experimental phase (last learning block vs. all testing blocks) in Figure 4.6A. Mixed-model ANOVAs were conducted to analyze the impairment effect resulted from the removal of different cues, with condition as a between-subject variable and experimental phase as a within-subject variable. The analysis revealed a main effect of experimental phase, F (1, 46) = 24.01, $p < .001$, $\eta_p^2 = .34$, but the interaction was not significant, F (1, 46) = .0001, $p = .99$, $\eta_p^2 < .001$, nor was the main effect of condition, F (1, 46) = .92, $p = .34$, $\eta_p^2 = .02$. Hence removing either of the two cues, the boundary or the outward landmark array, impaired localization during testing; and more importantly, the impairments resulting from the removal of either cue were on the same magnitude, as indicated by a lack of interaction. It is likely that both the boundary and the landmark array were relied upon equally as the reference points for encoding the four locations.

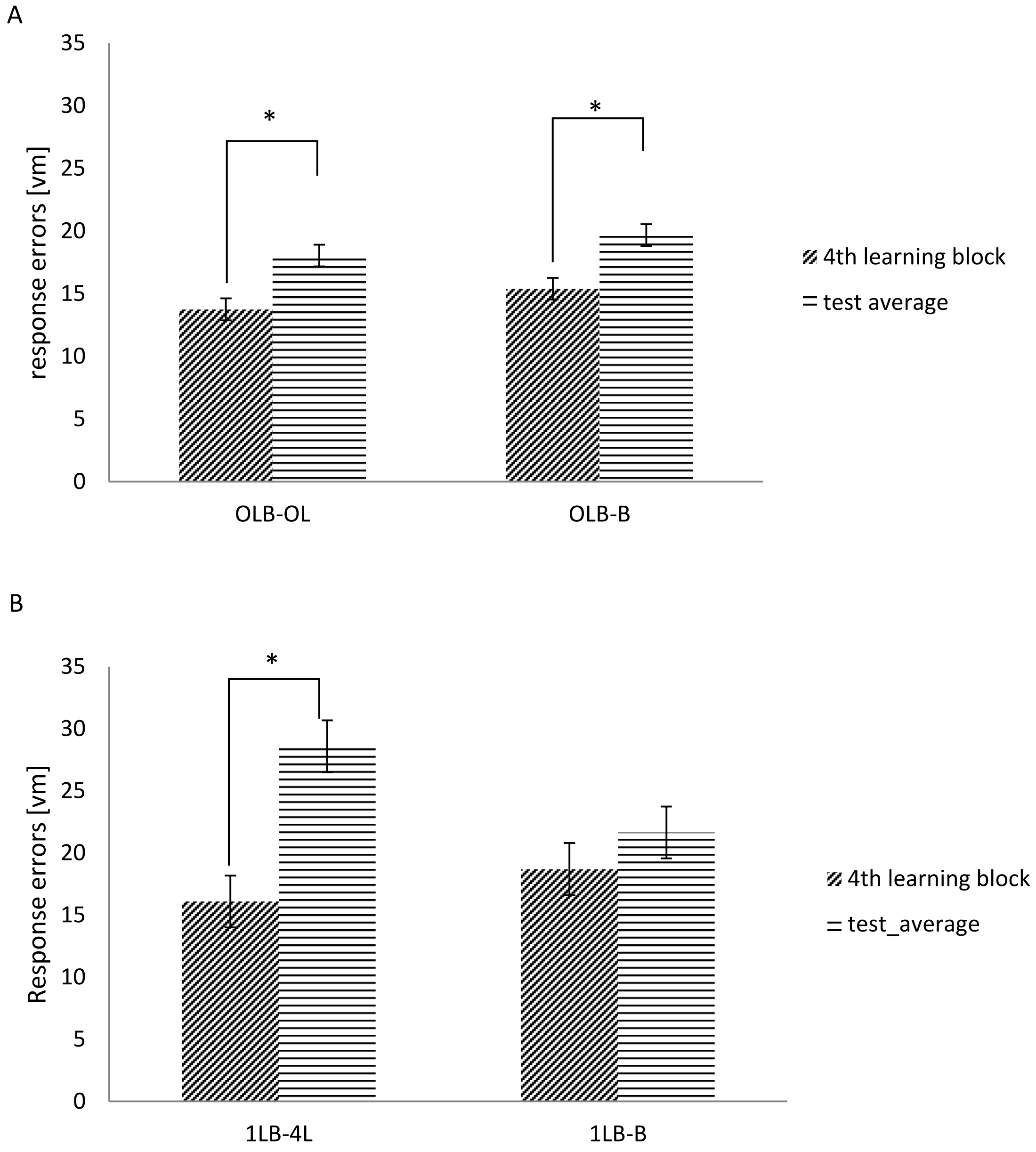


Figure 4.6. Response errors as a function of condition and experimental phase in Experiment 2 and 3 respectively. A, in Experiment 2; B, in Experiment 3. Error bars are ± 1 standard error.

4.5 Experiment 3

Experiment 2 demonstrated that increasing the perceived stability and distinctiveness of a landmark cue would raise the relative preference for the cue as a reference point for encoding locations. However, it is not clear whether distinctiveness alone could determine the modulation. In Experiment 3, we increased the distinctiveness of each traffic cone in the cone array but reduced the perceived stability of the cone array compared to those in Experiment 1. If the distinctiveness alone could explain the increased reliance upon the landmark cue in Experiment 2, we would expect a similar pattern of bi-directional overshadowing to result from removing either cue in the current experiment. Alternatively, if perceived stability is essential in modulating reference-point selection, we would expect a pattern similar to the boundary advantage found among the Doeller & Burgess' task group in Experiment 1.

Participants learned the locations of four objects with the presence of both a circular wall (the one presented in the Doeller & Burgess' task group in Experiment 1) and a landmark array consisting of four identical traffic cones (at the same locations as those used in Experiment 1). However the four cones were not presented simultaneously during each learning trial (Figure 4.5C). Instead, depending on the target location to be learned in a particular learning trial, one corresponding traffic cone (always the one that was closest to the target location among the four cones) would be presented together with a unique visual feature added on top of the cone. Therefore, the association between one landmark and one target location would not interfere with the association between another landmark and another target location. During the testing phase, one group was tested with the boundary alone; this condition was referred to as 1LB-B. The other group was tested with the four cones presented simultaneously (each traffic cone still had the unique visual feature on top to maintain its distinctiveness); this condition was referred to as 1LB-4L.

4.5.1 Method

Participants. Twenty-five students (12 males and 13 females) from the University of Alberta participated to fulfill a course requirement. One female participant was excluded, as her mean response error during testing was greater than 100 vm.

Materials, Design, and Procedure

The setup of Experiment 3 was identical to that of Experiment 1, with the following exceptions.

During the pick-up phase, the four cones were presented simultaneously, and each traffic cone had a small model of one of the four objects on top, which was used to make the each cone identifiable from the others. The identity of the small objects on top of each cone depended on the identity of the target object (the candle, the wood, the bottle or the lock) whose location was paired with the particular traffic cone. During the learning phase, at each trial, depending on the target location to be learned at the trial, only the corresponding traffic cone (the closest one among the four to this particular target location) would be presented together with the corresponding small object model on top of the cone. The circular wall as the boundary cue was also presented throughout the pick-up and the learning phase for each participant.

During the testing phase, one group of participants was tested with the boundary cue alone (the cone array removed); we refer to this group as LB-B. For the other group, denoted as

LB-L, the boundary cue was removed but the four traffic cones with their respective object models on top were presented throughout the testing phase.

4.5.2 Results and Discussion

The mean response errors are plotted as a function of experimental phase (the 4th learning block vs. all the testing blocks) and condition (LB-L vs. LB-B) in Figure 4.6B. Mixed-model ANOVAs were carried out to examine the impairment effect resulted from removing either cue during testing, with experimental phase as a within-subject variable and condition as a between-subject variable. An interaction between the variables was revealed, F (1, 22) = 5.21, p = .03, η_p^2 = .19, as well as a main effect of experimental phase, F (1, 22) = 13.65, p = .001, η_p^2 = .38. The main effect of condition was not significant, F (1, 22) = .7, p = .41, η_p^2 = .03. Planned comparisons indicated a significant increase in response errors during the testing phase of LB-L compared to the last learning block, t (11) = 4.23, p = .001, Cohen's d = 1.73 ($M_{\text{4th learning block}}$ = 16.08 vm, SD $M_{\text{4th learning block}}$ = 8.54; $M_{\text{testing average}}$ = 28.59 vm, SD $M_{\text{testing average}}$ = 11.19), whereas the response errors during testing were not significantly different from those during the last learning block in LB-B, t (11) = 1.00, p = .34, Cohen's d = .41 ($M_{\text{4th learning block}}$ = 18.69 vm, $SD_{\text{4th learning block}}$ = 6.72; $M_{\text{testing average}}$ = 21.65 vm, $SD_{\text{testing average}}$ = 4.76).

Thus, removing the boundary cue during testing impaired representations of the four locations; however, removing the landmark array did not have such an impairment effect on localization. This replicated the overshadowing effect of the boundary in the Doeller & Burgess' task group in Experiment 1. The results of Experiment 2 and 3 combined suggested that distinctiveness alone was not sufficient to modulate the relative preference assigned to a landmark cue and a boundary in encoding individual locations; the perceived stability of an environmental feature was critical in the evaluation of its usefulness as a potential reference point for encoding locations.

4.6 General Discussion

Three experiments were conducted to examine the potential factors contributing to the boundary advantage in encoding/representing individual locations, and in particular the perceived stability of an environmental feature and the distinctiveness of the potential reference points provided by the environmental feature for encoding a set of locations. Experiment 1 replicated both the boundary privilege in encoding individual locations (the boundary cue overshadowed the four-cone array but not vice-versa) and the landmark-array advantage in cognitive mapping in a single well-controlled experiment. Experiment 2 and 3 demonstrated that increasing the perceived stability of the landmark-array cue could increase the relative reliance upon the landmark cue when both the boundary and the landmark were available as potential reference points for encoding locations. However, increasing distinctiveness alone was insufficient to modulate the reference-point selection process.

The dissociation of a boundary cue and a landmark cue in terms of their respective advantages in encoding individual locations, and in forming cognitive maps of the locations, suggests that cognitive mapping might be a process independent from that of encoding individual locations. Boundary-related learning is thought to be hippocampus-dependent, whereas landmark-related learning is thought to be striatal-dependent (Doeller, King & Burgess, 2008). However, landmark-related learning was shown to benefit cognitive mapping in the current study (see also Zhou & Mou, 2016). This raises questions regarding the neural bases of the cognitive mapping process. Although it has long been proposed that the hippocampus is the major locus of forming cognitive maps (O'Keefe & Nadel, 1978), there is ongoing debate about whether the hippocampus is also responsible for the storage of such cognitive maps (Teng & Squire, 1999; Corkin, 2002; Moscovitch et al., 2005). One possibility is that cognitive mapping can also be achieved through non-hippocampal learning. Alternatively, the storage of cognitive maps could occur independently of the hippocampus. The novel-vector inference task employed in the current study directly tests the quality of cognitive maps derived from a particular localization cue, as the ability to infer novel spatial vectors is one critical function of cognitive maps (Levine, Jankovic, & Palij, 1982; Tolman, 1948). It would be worthwhile to investigate the neural substrates involved in conducting such cognitive mapping tasks.

Strikingly, the results of Experiment 2 showed that learning locations relative to a landmark array, which was placed close to the boundary, could impair the simultaneous learning of the same locations relative to a boundary cue. This finding challenges the proposal that boundary-related learning is incidental. Our result suggests that boundary-related learning might also be subject to the reference-point selection process, during which participants evaluate different environmental features to choose adequate reference points for encoding a particular location. Moreover, the relative reliance upon a certain environmental feature (or the relative weighting assigned to a certain environmental feature during reference-point selection) seems to be modulated by the physical characteristics of the feature, such as its perceived stability. In the current experiment, when the perceived stability of the four-cone array was increased, participants might have been more likely to evaluate the cones as adequate candidate reference points for encoding locations. As a result, bi-directional cue competition between the cone array and the circular boundary was observed.

Furthermore, the total computational resources devoted to learning locations relative to different environmental cues seems to be limited, as suggested by the reduced reliance upon the boundary cue when the relative stability of the boundary was decreased (increasing the relative stability of the landmark cue being equivalent to reducing the relative stability of the boundary) in the current study. This is in line with the associative model of geometry learning in reorientation (Buckley et al., 2014; Miller & Shettleworth, 2007). Abundant findings in reorientation literature have suggested that the geometric information provided by a surface boundary plays a privileged role in helping animals keep their bearings (for review of findings across different species, see Cheng & Newbombe, 2005). Thus, the learning of surface geometry provided by a boundary was thought to be exclusive of learning related to other environmental features. However, later evidence challenged the impenetrable characteristics of learning surface geometry, in that such learning was shown to be hindered or facilitated by learning of other environmental features (Buckley et al., 2014; Pearce, Graham, Good, Jones & McGregor, 2006; Wilson & Alexandar, 2008, 2010). Miller and Shettleworth adapted the Rescorla-Wagner model in associative learning to account for the inconsistent findings regarding cue competition between a boundary cue and other environmental features. According to their model, associative strength is assigned to enclosure geometry in terms of the probability that the cue can predict a reward location, and the strength is subject to competition from other environmental features.

Although the current task is a localization task, we propose that a similar weighting process also happens at the initial stage of localization, when people evaluate different environmental features according to the physical characteristics of the features and the navigational goal they have in mind. The idea of the cue evaluation process is in line with the adaptive combination model proposed by Newcombe and colleagues (Ratliff & Newcombe, 2008; see also Cheng, Huttenlocher, & Newcombe, 2013). For instance, a stable environmental feature will be evaluated as a better reference point for encoding a target location. Once the environmental cues are selected as reference points for encoding locations, computational resources are devoted to spatial learning relative to the chosen reference point. Such an evaluation and reference-selection process is also involved in boundary learning. In the present study, therefore, when the landmark array was evaluated as a competitive cue for localization (such as being perceived as more stable), less weighting might have been assigned to encoding relative to the boundary, which led to an overshadowing effect from the landmark array over the boundary. The current study only used a circular boundary and manipulated the relative stability between the two cues. Future studies are needed to look into other factors that could modulate the reference-point selection process, such as the shape of the boundary or the configuration of the landmark array.

In conclusion, the current study demonstrated a boundary advantage in encoding individual locations as well as a landmark advantage in cognitive mapping (Experiment 1). Moreover, we found that perceived relative stability can modulate the boundary advantage in encoding individual locations (Experiment 2 and 3)—that is, increasing the perceived relative stability of a landmark array induces an effect in which the landmark overshadows a boundary, and the magnitude of such an overshadowing effect is equivalent to that from the boundary cue, demonstrating that the two cues compete equally for the computational resources assigned to learning them.

4.7 References

Anderson, M. C. (2003). Rethinking interference theory: Executive control and the mechanisms of forgetting. *Journal of Memory and Language*, *49*, 415-445.

Barry, C., Lever, C., Hayman, R., Hartley, T., Burton, S., O'Keefe, J., Jeffery, H., & Burgess, N. (2006). The boundary vector cell model of place cell firing and spatial memory. *Reviews in the Neurosciences*, *17*(1-2), 71-97.

Bennett, A. T. D. (1996). Do animal have cognitive maps. *The Journal of Experimental Biology*, *199*, 219-224.

Bird, C. M., Capponi, C., King, J. A., Doeller, C. R., & Burgess, N. (2010). Establishing the boundaries: the hippocampal contribution to imagining scenes. *The Journal of Neuroscience, 30*(35), 11688-11695.

Buckley, M. G., Smith, A. D., & Haselgrove, M. (2014). Shape Shifting: Local Landmarks Interfere With Navigation by, and Recognition of, Global Shape. *Journal of Experimental Psychology: Learning, Memory and Cognition*, *40*(2), 492-510.

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

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

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

Cheng, K. (1989). The vector sum model of pigeon landmark use. *Journal of Experimental Psychology: Animal Behavior Processes, 15*(4), 366-375.

Cheng, K., Huttenlocher, J., & Newcombe, N. (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), 1-23.

Cressant, A., Muller, R. U., & Poucet, B. (1997). Failure of centrally placed objects to control the firing fields of hippocampal place cells. The Journal of Neuroscience, 17, 2531–2542.

Doeller, C. F., & Burgess, N. (2008). Distinct error-correcting and incidental learning of location relative to landmarks and boundaries. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(15), 5909-5914.

Doeller, C. F., King, J. A., & Burgess, N. (2008). Parallel striatal and hippocampal systems for landmarks and boundaries in spatial memory. *Proceedings of the National Academy of Sciences of the United States of Americ*a, *105*(15), 5915-5920.

Ekstrom, A. D., Kahana, M. J., Caplan, J. B., Fields, T. A., Isham, E. A., Newman, E. L., & Fried, I. (2003). Cellular networks underlying human spatial navigation. *Nature*, *425*, 184-188.

Hamilton, D. A., Akers, K. G., Weisend, M. P., & Sutherland, R. J. (2007). How do room and apparatus cues control navigation in the Morris Water Task? Evidence for distinct contributions to a movement vector. *Journal of Experimental Psychology: Animal Behavior Processes, 33*(2), 100-114.

Hartley, T., Burgess, N., Lever, C., Cacucci, F., & O'Keefe, J. (2000). Modeling place fields in terms of the cortical inputs to the hippocampus. *Hippocampus, 10*, 369-379.

Hartley, T., Maguire, E. A., Spiers, H. J., & Burgess, N. (2003). The well-worn route and the path less traveled: Distinct neural bases of route following and wayfinding in humans. *Neuron*, *37*, 877-888.

Hartley, T., Trinkler, I., & Burgess, N. (2004). Geometric determinants of human spatial memory. *Cognition*, *94*(1), 39-75.

Iaria, G., Petrides, M., Dagher, A., Pike B., & Bohbot, V. D. (2003). Cognitive strategies dependent on the hippocampus and caudate nucleus in human navigation: Variability and change with practice. *The Journal of Neuroscience*, *23*(13), 5945-5952.

Jeffery, K. J. (1998). Learning of landmark stability and instability by hippocampal place cells. *Neurophamacology*, *37*, 677-687.

Knierim, J. J., Kudrimoti, H. S., & McNaughton, B. L. (1995). Place cells, head direction cells, and the learning of landmark stability. *Journal of Neuroscience*, *15*(3), 1648–1659.

Lever, C., Burtonm S., Jeewajee, A., O'Keefe, J., & Burgess, N. (2009). Boundary vector cells in the subiculum of the hippocampal formation. *Journal of Neuroscience, 29*(31), 9771-9777.

Levine, M., Jankovic, I. N., & Palij, M. (1982). Principles of spatial problem solving. *Journal of Experimental Pscyhology: General*, *111*(2), 157-175.

Lew, A. R. (2011). Looking Beyond the Boundaries: Time to put Landmarks back on the cognitive map? *Psychological Bulletin, 137*(3), 454-507.

Marchette, S. A., Bakker, A., & Shelton, A. L. (2011). Cognitive mappers to creatures of habit: Differentail engagement of place and response learning mechanisms predicts human navigational behavior. *The Journal of Neuroscience*, *31*(43), 15264-15268.

McDonald, R. J., & White, N. M. (1994). Parallel information processing in the water maze: evidence for independent memory systems involving dorsal striatum and hippocampus. *Behavioral Neural Biology*, *61*(3), 260-270.

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

Morris, R. G. M. (1981). Spatial localization does not require the presence of local cues. *Learning and Motivation*, *12*, 239-260.

Morris, R. G. M. (1982). Place navigation impaired in rats with hippocmpal lesions. *Nature*, *297*, 681-683.

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), 1115-1127.

Nadel, L. (2013). Cognitive maps. In D. Waller & L. Nadel (Eds.), *Handbook of spatial cognition* (pp. 155-171). Washington, DC, US: American Psychological Association.

Newcombe, N. S., & Ratliff, K.R. (2007). Explaining the development of spatial reorientation: Modularity-plus-language versus the emergence of adaptive combination. In J. Plumert & J. Spencer (eds.), *The emerging spatial mind* (pp. 53–76). Oxford: Oxford University Press.

O'Keefe, J., & Burgess, N. (1996). Geometric determinants of the place fields of hippocampal neurons. *Nature, 381*, 425-428.

O'Keefe, J., & Dostrovsky, J. (1971). The hippocampus as a spatial map. Preliminary evidence from unit activity in the freely-moving rat. *Brain Research*, *34*, 171-175.

O'Keefe, J. (1976). Place Units in the Hippocampus of the Freely Moving Rat. *Experimental Neurology*, *51*, 78-109.

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

Parkard, M. G., & McGaugh, J. L. (1992). Double dissociation of fornix and caudate nucleus lesions on acquisition of two Water Maze Tasks: Further evidence for multiple memory systems. *Behavioral Neuroscience, 106*(3), 439-446.

Pearce, J. M., Graham, M., Good, M. A., Jones, P. M., & McGregor, A. (2006). Potentiation, overshadowing, and blocking of spatial learning based on the shape of the environment. *Journal of Experimental Psychology: Animal Behavior Processes, 32*(3), 201-214.

Pearce, J. M., Roberts, A. D. L., & Good, M. (1998). Hippocampal lesions disrupt navigation based on cognitive maps but not heading vectors. *Nature*, *396*, 75-77.

Ratliff, K. R., & Newcombe, N. S. (2008). Reorienting when cues conflict: evidence for an adaptive-combination view. *Psychological Science, 19*(12), 1301-1307.

Redish, A. D. (1999). *Beyond the cognitive map: From place cells to episodic memory*. The MIT Press.

Spetch, M. L. (1995). Overshadowing in landmark learning: Touch-screen studies with pigeons and humans. *Journal of Experimental Psychology: Animal Behavioral Processes, 21*(2), 166-181.

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

Wilson, P. N., & Alexander, T. (2008). Blocking of spatial learning between enclosure geometry and a local landmark. *Journal of Experimental Psychology: Learning Memory and Cognition, 34*(6), 1369-1376.

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

Zhou, R., & Mou, W. (2016). Superior cognitive mapping through single landmark-related learning than through boundary-related learning. *Journal of Experimental Psychology: Learning, Memory and Cognition*. In press

Chapter 5

Summary and General Discussion

5.1 Summaries

The first major goal of the work carried out in the thesis is to understand the roles of different types of environmental features in the course of developing a cognitive map, from encoding individual locations to cognitive mapping of multiple locations. More specifically, we demonstrated a landmark advantage (either a single landmark in Chapter 2 or a four-landmark array in Chapter 3 and 4) in cognitive mapping of integrating individual-location representations and a surface-boundary advantage in encoding individual locations (Chapter 4). We then further investigated what gave rise to a landmark advantage in cognitive mapping (or in other words what impaired the cognitive mapping relative a boundary cue) and to a boundary advantage in encoding/representing individual location, respectively. The studies in Chapter 3 identified two factors that impeded cognitive mapping relative to a circular boundary: 1) that multiple reference points were chosen for encoding a set of locations (each location encoded relative to its own unique reference point, thus a lack of common reference point) and as a result, integrating individual representations of the multiple location was more challenging; 2) that a lack of knowledge about the direct spatial relations among the chosen reference point from the boundary impaired cognitive mapping relative to the boundary. In Chapter 4, we set out to investigate why a boundary cue is preferred over a landmark cue (a single landmark or a landmark array) in encoding individual locations and we demonstrated that perceived relative stability of an environmental feature could modulate cue preference when participants are choosing reference points among multiple environmental features.

5.2 Main Findings and Discussions

5.2.1 Visual environmental features in forming cognitive maps

Chapter 2 demonstrated that an object-based landmark, rather than a circular boundary, benefitted cognitive mapping of multiple locations. Participants learned the locations of four objects sequentially (learning one location at a time) either relative to a circular boundary or a single landmark (a traffic cone presented as the landmark cue) while distal orientation cues provided allocentric directions of the environment. Two cognitive mapping tasks were employed to assess the relative quality of the cognitive maps of the four locations derived from either cue. In particular, knowledge of direct spatial relations between two of the four locations was assessed in Experiment 1 and knowledge of configuration among three of the four locations was assessed in Experiment 2. Since one important function of a cognitive map is to assist inference of novel spatial relations among locations registered in the map, we consider performance on the two tasks could reflect the quality of the acquired cognitive maps in respective conditions. In both experiments, participants' performance was superior when the locations were encoded relative to the landmark than to the boundary.

The reason we focus on these two types of localization cues is that spatial learning relative to the two types of environmental features are thought to involve two distinctive learning systems, respectively. In particular, encoding a target location relative to a boundary cue is proposed to engage the place learning system supported by the hippocampal formation (Doeller & Burgess, 2008) whereas encoding a target location relative to a landmark based on discrete objects is proposed to be processed by the response learning system supported by the striatum. Hence the real question we are asking in Chapter 2 is how these two learning/memory systems contribute to forming a cognitive map of an environment. Cognitive map theories postulate that the hippocampal-dependent place-learning system would be critical in forming a cognitive map of a given environment and the hippocampus itself is likely the responsible for acquiring and storing the cognitive map. Therefore according to the theories, learning locations relative to the boundary cue should yield a more accurate cognitive map than learning relative to the landmark cue. However the current finding demonstrated an opposite pattern of results.

One possible explanation for inconsistency between the current results and the speculation from cognitive map theories is that learning locations relative to the landmark in the current study might be beyond simple stimulus-response association. In the current study, to locate the four objects as accurately as possible, one has to encode the exact spatial relation between each location and the landmark. In this case, the landmark is no longer a signal for a certain action but rather serving as a reference point upon which a spatial vector could be established to identify a target location. Indeed the equivalent accuracy in locating the four objects relative to either cue in the last learning block indicated that participants in the landmark condition did acquire the "place" information of the objects, just as those in the boundary condition did. Our vector-addition model further posits that a more accurate cognitive map of multiple locations would be yielded when all the locations are encoded relative to a common reference point rather than when the locations are encoded relative to different reference points. Hence the single landmark serving as the common reference point for the four locations led to a better cognitive map. In contrast, the circular boundary providing multiple reference points might be inferior cue for cognitive mapping.

The findings in Chapter 2 also raise some question regarding the role of hippocampus in different aspects of forming a cognitive map. Extending from their multiple trace theory, Moscovitch and Nadel (Moscovitch et al., 2005; Nadel, Samsonovich, Ryan & Moscovitch, 2000) proposed that long-term spatial representation entails detail spatial memory (similar to the concept of episodic memory, allowing for re-experiencing the environment) as well as more semantic spatial memory (similar to the concept of semantic memory); and the two types of memories might have differential dependence on the hippocampal function. That is, the detailed, episodic-like spatial memory is represented in the hippocampus whereas the semantic-like spatial memory in extra-hippocampal structures. Concurring with this theory, accumulating research evidence has pointed out a significant role of the retrosplenial cortex in allocentric spatial representation of a given environment by processing the spatial relations among environmental features (e.g., Parron & Save, 2004; Wolber & Buchel, 2005; Vass & Epstein, 2013; for review, see Miller, Vedder, Law & Smith, 2014). Hence we speculate that the two spatial tasks employed (assessing knowledge about spatial relations between two or among three objects) in Chapter 2 might tap into the more semantic aspect of spatial memory and thus, are less reliant on the hippocampal place-learning system (such as learning relative to a boundary cue).

Chapter 3 is built upon the findings from Chapter 2 in that we investigated potential factors impeding cognitive mapping relative to a continuous circular boundary. Our previous work suggests that a circular boundary might be functionally equivalent to a collection of multiple reference points when used as a spatial cue for specifying locations (Mou & Zhou, 2013). Furthermore we hypothesized that when participants are navigating themselves within a circular boundary surrounded by distal orientation cues, the boundary was segmented into pieces that are differentiated by the distal orientation cues (e.g., "I am currently at the edge closer to the Ocean direction"). We refer to this process as the segmentation process, the function of which is to keep one oriented in a given space (e.g., a circular space). To encode a specific location relative to the boundary, participants then choose a boundary segment that has the closest distance to the target location as the optimal reference point. We refer to this process as the reference-point selection process. Thus, a circular boundary provided multiple reference points for encoding a set of multiple locations and each location would have its own reference point. Integrating such separate location memories (each location represented relative to its respective reference point) would be more challenging than integrating location memories sharing a common source (i.e., specified by a common reference point). In the first experiment of Chapter 3 we compared the relative accuracy of cognitive maps derived from a single wall segment, from four optimal wall segments and from the whole circular boundary. The results demonstrated that cognitive mapping performance decreased as the number of reference points increased, supporting our speculation.

Another critical factor that impeded cognitive mapping relative to the circular boundary is a lack of knowledge about the direct spatial relation among the chosen reference points, as indicated by Experiment 2 in Chapter 3. The cognitive mapping performances were significantly impaired when the direct spatial relations among the optimal wall segments were made less acceeessible as compared to the condition where the spatial relations among the segments were directly perceivable. Combining the results of the two experiments, we draw upon an implication that when localizing within a bounded space, one seems to segment the space into different parts (e.g., the circular boundary were segmented into pieces) and only the most relevant part of the environment to one's current navigation task is paid attention do (e.g., choosing the optimal reference points from all the segments). The spatial relations among the separate parts however are not actively encoded. Therefore we conclude that the global space enclosed by a boundary might be represented in a fragmented fashion in a goal localization task. This is in contrast in the representation of an enclosed space in a reorientation task in that the global shape of the bounded space is thought to be an important cue for an individual to gain their bearings (Cheng, 1986;

Gallistel, 1990). The finding that a circular space was parsed into separate regions in a goal localization task suggests that localization (or encoding locations within an environment) might be a separate process from orientation as an individual mainly attends to a limited part of the space that is relevant to the current spatial task.

5.2.2 Place learning and response learning revisited

In the first experiment of Chapter 4, we demonstrated the privileged role of a circular boundary over a four-landmark array in encoding a set of four locations sequentially (overshadowing effect of the boundary over the landmark array) as well as the landmark-array advantage in forming a more accurate cognitive map of the four locations. The result was inconsistent with the different privileged roles of the two cues in different spatial tasks (Doeller & Burgess, 2008; Zhou & Mou, 2016). Note that the privileged role of the boundary cues in spatial learning of individual locations does not lend to more accurate representations of individual locations compared to the landmark cues (as shown in the equivalent localization performances relative the boundary and the single landmark in Zhou & Mou, 2016; see also Doeller & Burgess, 2008). Therefore we aim to understand why a boundary cue is preferred as reference point for encoding locations even though the cue is not necessarily a more reliable cue for more accurate spatial representations.

We hypothesize that upon encountering an environment, one evaluates the usefulness/the validity of various environmental features in order to complete a given navigation task. In the task of encoding a specific location, a stable and a distinctive visual feature in the environment might be perceived as a more reliable/valid cue to be used as the reference point for encoding the target location. We refer this process as the reference-point selection process (the proposal shares some idea with adaptive cue combination model proposed by Newcombe and colleagues to explain the cue competition process in reorientation; see Ratliff & Newcombe, 2008). As a result of this selection process, different weights (or reliance) are assigned to the evaluated features. The more weights assigned to a particular feature would determine more computation resources designated to the feature. We speculate that surface-based boundary cue would be subject to this selection process as well as landmark cues. A boundary enclosing the environment might be perceived as more stable than a single object and thus, would be assigned more weights as a reference point for encoding a target location, leading to the boundary advantage in encoding individual locations. In Experiment 2 and 3 of Chapter 4, we manipulated the perceived relative stability of the boundary and the landmark array as well as the distinctiveness of the potential reference points provided by the two cues. The results demonstrated that the landmark array with increased stability overshadowed the boundary cue however increasing the distinctiveness of the landmark array alone was not sufficient to induce the overshadowing effect of the landmark array. The results suggest that even a boundary cue is subjected to the reference-point selection process, thus not immune to cue competition.

The findings that a boundary cue can be overshadowed by a landmark-array cue is contradictory to the proposal that place learning is latent and incidental (Tolman, 1948; Nadel, 2013; Doeller & Burgess, 2008) as encoding locations relative to a boundary is considered as a form of place learning (Doeller & Burgess, 2008). The results of Chapter 4 challenge the non-associative nature of place learning (e.g., the immunity to cue competition). Indeed, some previous research has cast doubt on the non-associative property of place learning, the findings of which demonstrated blocking, overshadowing and potentiation in place learning (e.g., Hamilton & Shettleworth, 1999; Roberts & Pearce, 1999; Pearce, Graham, Good, Jones & McGregor, 2006; see also Kelly & Gibson, 2007).

5.3 Future Research

The two cognitive mapping tasks employed in Chapter 2 of the current thesis are thought to directly assess the quality of a cognitive map derived from a specific localization cue. The first task requires one to infer novel spatial relations between two locations and the second task require one to infer spatial configuration among three locations. The assessed knowledge cannot be directly acquired from the spatial representation encoded during the learning phase but one has to infer from integrating the representations of individual locations. The ability to infer novel spatial relations is a defining property of a cognitive map. Hence it might be worthwhile to employ cognitive mapping tasks such as the two used in Chapter 2 in neural imaging studies in order to gain more insight into the underpinning neural substrates involved in forming and storing cognitive maps.

The incidental and latent characteristics of cognitive maps implies that the acquisition and integration of some new information into the existing spatial knowledge of a cognitive map would be automatic (i.e., one would always automatically incorporate new spatial information into the current cognitive maps). Thus, another interesting question regarding the formation of cognitive maps might be how automatic this updating process would be. According to the results of the current thesis, it seems that one might not actively incorporate the representation of individual locations as localization relative to a boundary seemed to be processed in a fragmented fashion. Thus, do we compute novel spatial relations just on the fly or can we ultimately acquire and store a unified “mental map” of a large scale environment? In future research, the cognitive mapping knowledge could be probed at different time points of spatial learning (such as giving the cognitive mapping tasks after different numbers of learning trials during which participants are learning the individual locations) so as to assess the developing curve of the cognitive maps. On the other hand, participants can also be made aware of the cognitive mapping tasks beforehand (as in the current thesis participants were never aware beforehand that their cognitive map knowledge would be tested) and the quality of the cognitive maps under such condition would be superior to that from the "innocent" participants.

The boundary used in the current studies included in the thesis was a circular homogenous wall, which would be rarely seen in a natural setting. Future research could tap into localization and cognitive mapping relative to boundaries of irregular shapes, which would extend the current findings into more real-life scenarios.

Environmental features are vital for successful navigation of an individual which in turn is critical for an individual's survival and wellbeing through the life course. Understanding the roles played by various visual features in the course of developing a cognitive map of the surroundings would allow insight into how different learning mechanisms engage in and contribute to our mental maps.

5.4 Reference

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

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.

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

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

Kelly, D. M., & Gibson, B. M. (2007). Spatial Navigation: Spatial learning in real and virtual environments. *Comparative Cognition & Behavior Reviews, 2*, 111-124.

Miller, A. M., Vedder, L. C., Law, L. M., & Smith, D. M. (2014). Cues, context, and long-term memory: the role of the retrosplenial cortex in spatial cognition. *Frontiers in Human Neuroscience*, *8*: 586. doi: 10.3389/fnhum.2014.00586.

Moscovitch, M., Rosenbaum, R. S., Gilboa, A., Addis, D. R., Westmacott, R., Grady, C., McAndrews, M. P., Levine, B., Black, S., Winocur, G., & Nadel, L. (2005). Functional neuroanatomy of remote episodic, semantic and spatial memory: a unified account based on multiple trace theory. *Journal of Anatomy*, *207*, 35-66.

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), 1115-1127.

Nadel, L., Samsonovich,, A., Ryan, L., & Moscovitch, M. (2000). Multiple trace theory of human memory: computational, neuroimaging, and neuropsychological results. *Hippocampus, 10*(4), 352-368.

Nadel, L. (2013). Cognitive maps. In D. Waller & L. Nadel (Eds.), *Handbook of spatial cognition* (pp. 155-171). Washington, DC, US: American Psychological Association.

Parron, C., & Save, E. (2004). Comparison of the effects of entorhinal and retrosplenial cortical lesions on habituation, reaction to spatial and non-spatial changes during object exploration in the rat. *Neurobiology of Learning and Memory, 82*, 1-11.

Pearce, J. M., Graham, M., Good, M. A., Jones, P. M., & McGregor, A. (2006). Potentiation, overshadowing, and blocking of spatial learning based on the shape of the environment. *Journal of Experimental Psychology: Animal Behavior Processes, 32*(3), 201-214.

Ratliff, K. R., & Newcombe, N.S. (2008). Reorienting when cues conflict: evidence for an adaptive-combination view. *Psychological Science, 19*, 1301-1307.

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

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

Vass, L. K. & Epstein, R. A. (2013). Abstract representations of location and facing direction in the human brain. *Journal of Neuroscience*, *33*(14), 6133-6142.

Wolbers, T., & Büchel, C. (2005). Dissociable retrosplenical and hippocampal contributions to successful formation of survey representations. *The Journal of Neuroscience*, *25*(13), 3333-3340.

Zhou, R., & Mou, W. (2016). Superior cognitive mapping through single landmark-related learning than through boundary-related learning. Journal of Experimental Psychology: Learning, Memory and Cognition. In press.

Bibliography

Aguirre, G. K., & D'Esposito, M. (1997). Environmental knowledge is subserved by separable dorsal/ventral neural areas. *The Journal of Neuroscience*, *17*(7), 2512-2518.

Anderson, M. C. (2003). Rethinking interference theory: Executive control and the mechanisms of forgetting. *Journal of Memory and Language*, *49*, 415-445.

Barry, C., Lever, C., Hayman, R., Hartley, T., Burton, S., O'Keefe, J., Jeffery, H., & Burgess, N. (2006). The boundary vector cell model of place cell firing and spatial memory. *Reviews in the Neurosciences*, *17*(1-2), 71-97.

Barry, C., & Burgess, N. (2007). Learning in a geometric model of place cell firing. *Hippocampus*, *17*(9), 786-800.

Bennett, A. T. D. (1996). Do animal have cognitive maps. *The Journal of Experimental Biology*, *199*, 219-224.

Bird, C. M., Capponi, C., King, J. A., Doeller, C. R., & Burgess, N. (2010). Establishing the boundaries: the hippocampal contribution to imagining scenes. *The Journal of Neuroscience, 30*(35), 11688-11695.

Bohbot, V. D., Kaline, M., Stepankova, K., Spackova, N., Petrides, M., & Nadel, L. (1998). Spatial memory deficits in patients with lesions to the right hippocampus and to the right parahippocampal cortex. *Neuropsychologia*, *36*(11), 1217-1238.

Buckley, M. G., Smith, A. D., & Haselgrove, M. (2014). Shape Shifting: Local Landmarks Interfere With Navigation by, and Recognition of, Global Shape. *Journal of Experimental Psychology: Learning, Memory and Cognition*, *40*(2), 492-510.

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

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

Brandeis, R., Brandys, Y., & Yehuda, S. (1989). The use of the Morris Water Maze in the study of memory and learning. *International Journal of Neuroscience, 48*, 29-69.

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

Cheng, K. (1989). The vector sum model of pigeon landmark use. *Journal of Experimental Psychology: Animal Behavior Processes, 15*(4), 366-375.

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*, 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), 1-23.

Cheng, K., & Spetch, M. L. (1998). Mechanisms of landmark use in mammals and birds. In S. Healy (Ed.). Spatial Representation in Animals, Oxford: Oxford University Press, pp. 1-17.

Cheung, A., Sturzl, W., Zeli, J. (2008). The Information Content of Panoramic Images II: View-based navigation in nonrectangular experimental arenas. *Journal of Experimental Psychology: Animal Behavior Processes, 34*(1), 15-30.

Collett, T. S., Cartwrigth, B. A., & Smith, B. A. (1986). Landmark learning and visuo-spatial memories in gerbils. Journal of Comparative Physiology, 158, 835-851.

Corkin, S. (2002). What's new with the amnesic patient H. M.? *Nature Reviews Neuroscience*, *3*, 153-160.

Cressant A., Muller, R. U., & Poucet, B. (1997). Failure of centrally placed objects to control the firing fields of hippocampal place cells. *The Journal of Neuroscience*, *17*, 2531–2542.

Doeller, C. F., & Burgess, N. (2008). Distinct error-correcting and incidental learning of location relative to landmarks and boundaries. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(15), 5909-5914.

Doeller, C. F., King, J. A., & Burgess, N. (2008). Parallel striatal and hippocampal systems for landmarks and boundaries in spatial memory. *Proceedings of the National Academy of Sciences of the United States of Americ*a, *105*(15), 5915-5920.

Ekstrom, A. D., Kahana, M. J., Caplan, J. B., Fields, T. A., Isham, E. A., Newman, E. L., & Fried, I. (2003). Cellular networks underlying human spatial navigation. *Nature*, *425*, 184-188.

Epstein, R. A., & Vass, L. K. (2014). Neural systems for landmark-based wayfinding in humans. *Philosophical Transactions of the Royal Society Biological Sciences*, *369*(1635), 20120533.

Evans, G. W., & Pezdek, K. (1980). Cognitive mapping: Knowledge of real world distance and location information. *Journal of Experimental Psychology: Human Learning and Memory*, *6*, 13-24.

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

Gouteux, S., & Spelke, E. S. (2001). Children's use of geometry and landmarks to reorient in an open space. *Cognition, 81*, 119-148.

Hamilton, D. A., Akers, K. G., Weisend, M. P., & Sutherland, R. J. (2007). How do room and apparatus cues control navigation in the Morris Water Task? Evidence for distinct contributions to a movement vector. *Journal of Experimental Psychology: Animal Behavior Processes, 33*(2), 100-114.

Hartley, T., Burgess, N., Lever, C., Cacucci, F., & O'Keefe, J. (2000). Modeling place fields in terms of the cortical inputs to the hippocampus. *Hippocampus, 10*, 369-379.

Hartley, T., Maguire, E. A., Spiers, H. J., & Burgess, N. (2003). The well-worn route and the path less traveled: Distinct neural bases of route following and wayfinding in humans. *Neuron*, *37*, 877-888.

Hartley, T., Trinkler, I., & Burgess, N. (2004). Geometric determinants of human spatial memory. *Cognition*, *94*(1), 39-75.

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

Iaria, G., Petrides, M., Dagher, A., Pike B., & Bohbot, V. D. (2003). Cognitive strategies dependent on the hippocampus and caudate nucleus in human navigation: Variability and change with practice. *The Journal of Neuroscience*, *23*(13), 5945-5952.

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*, 93-129.

Janzen, G., & van Turennout, M. (2004). Selective neural representation of objects relevant for navigation. *Nature Neuroscience*, *7*, 673–677.

Jeffery, K. J. (1998). Learning of landmark stability and instability by hippocampal place cells. *Neurophamacology*, *37*, 677-687.

Kamil, A. C., & Cheng, K. (2001). Way-finding and landmarks: the multiple-bearings hypothesis. *Journal of Experimental Biology, 204*, 103-113.

Kamin. L. J. Attention-like processes in classical conditioning. In M. R. Jones (Ed.), Miami Symposium on the prediction of behavior: Aversive stimulation. Miami: Universily of Miami Press, 1968.

Kelly, D. M., & Gibson, B. M. (2007). Spatial Navigation: Spatial learning in real and virtual environments. *Comparative Cognition & Behavior Reviews, 2*, 111-124.

Klatzky, R. L. (1998). Allocentric and egocentric spatial representations: Definitions, distinctions, and interconnections. In C. Freksa, C. Habel, & K. F. Wender (Eds.), *Spatial cognition - An interdisciplinary approach to representation and processing of spatial knowledge* (Lecture Notes in Artificial Intelligence 1404) (pp. 1-17). Berlin: Springer-Verlag.

Knierim, J. J., Kudrimoti, H. S., & McNaughton, B. L. (1995). Place cells, head direction cells, and the learning of landmark stability. *Journal of Neuroscience*, *15*(3), 1648–1659.

Knierim, J., & Hamilton, D. A. (2010). Framing spatial cognition: neural representation of proximal and distal frames of reference and their roles in navigation. *Physiological Reviews, 91*, 1245-1279.

Konkle, T., & Oliva, A. (2012). A real-world size organization of object responses in occipitotemporal cortex. *Neuron*, *74*, 1114–1124.

Lever, C., Burtonm S., Jeewajee, A., O'Keefe, J., & Burgess, N. (2009). Boundary vector cells in the subiculum of the hippocampal formation. *Journal of Neuroscience, 29*(31), 9771-9777.

Levine, M., Jankovic, I. N., & Palij, M. (1982). Principles of spatial problem solving. *Journal of Experimental Pscyhology: General*, *111*(2), 157-175.

Lew, A. R. (2011). Looking Beyond the Boundaries: Time to put Landmarks back on the cognitive map? *Psychological Bulletin, 137*(3), 454-507.

Maguire, E. A., Frackowiak, R. S. J., & Frith, C. D. (1996). Learning to find your way: a role for the human hippocampal region. *Proceedings of Royal Society London [Biology], 263*, 1745–1750.

Maguire, E. A., Frackowiak, R. S. J., & Frith, C. D. (1997). Recalling Routes around London: Activation of the Right Hippocampus in Taxi Drivers. *Journal of Neuroscience, 17*(18), 7103-7110.

Maguire, E. A., Nannery, R., & Spiers, H. J. (2006). Navigation around London by a taxi driver with bilateral hippocampal lesions. *Brain*, *129*, 2894-2907.

Marchette, S. A., Bakker, A., & Shelton, A. L. (2011). Cognitive mappers to creatures of habit: Differentail engagement of place and response learning mechanisms predicts human navigational behavior. *The Journal of Neuroscience*, *31*(43), 15264-15268.

McDonald, R. J., & White, N. M. (1994). Parallel information processing in the water maze: evidence for independent memory systems involving dorsal striatum and hippocampus. *Behavioral Neural Biology*, *61*(3), 260-270.

Miller, A. M., Vedder, L. C., Law, L. M., & Smith, D. M. (2014). Cues, context, and long-term memory: the role of the retrosplenial cortex in spatial cognition. *Frontiers in Human Neuroscience*, *8*: 586. doi: 10.3389/fnhum.2014.00586.

MvGauran, A.T., Harvey, D., Cunningham, L., Craig, S., & Commins, S. (2004). Retention of cue-based associations in the water maze is time-dependent and sensitive to disruption by rotating the starting position. *Behavioral brain research, 151*, 255-266.

Morris, R. G. M. (1981). Spatial localization does not require the presence of local cues. *Learning and Motivation*, *12*, 239-260.

Morris, R. G. M. (1982). Place navigation impaired in rats with hippocmpal lesions. *Nature*, *297*, 681-683.

Moscovitch, M., Rosenbaum, R. S., Gilboa, A., Addis, D. R., Westmacott, R., Grady, C., McAndrews, M. P., Levine, B., Black, S., Winocur, G., & Nadel, L. (2005). Functional neuroanatomy of remote episodic, semantic and spatial memory: a unified account based on multiple trace theory. *Journal of Anatomy*, *207*, 35-66.

Mou, W., Nankoo, J., Zhou, R., & Spetch, M. L. (2013). Use of geometric properties of landmark arrays for reorientation relative to remote cities and local objects. *Journal of Experimental Psychology: Learning, Memory and Cognition, 40*(2), 476-491.

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), 1115-1127.

Mullally, S. L., & Maguire, E. A. (2011). A new role for the parahippocampal cortex in representing space. *Journal of Neuroscience*, *31*, 7441–7449.

Nadel, L. (2013). Cognitive maps. In D. Waller & L. Nadel (Eds.), *Handbook of spatial cognition* (pp. 155-171). Washington, DC, US: American Psychological Association.

Nadel, L., & Moscovitch, M. (1997). Memory consolidation, retrograde amnesia and the hippocampal complex. *Current Opinion of Neurobiology*, *7*, 217–227.

Newcombe, N. S., & Ratliff, K. R. (2007). Explaining the development of spatial reorientation: Modularity-plus-language versus the emergence of adaptive combination. In J. Plumert & J. Spencer (eds.), *The emerging spatial mind* (pp. 53–76). Oxford: Oxford University Press.

O'Keefe, J., & Burgess, N. (1996). Geometric determinants of the place fields of hippocampal neurons. *Nature, 381*, 425-428.

O'Keefe, J., & Dostrovsky, J. (1971). The hippocampus as a spatial map. Preliminary evidence from unit activity in the freely-moving rat. *Brain Research*, *34*, 171-175.

O'Keefe, J. (1976). Place Units in the Hippocampus of the Freely Moving Rat. *Experimental Neurology*, *51*, 78-109.

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

Parkard, M. G., & McGaugh, J. L. (1992). Double dissociation of fornix and caudate nucleus lesions on acquisition of two Water Maze Tasks: Further evidence for multiple memory systems. *Behavioral Neuroscience, 106*(3), 439-446.

Parron, C., & Save, E. (2004). Comparison of the effects of entorhinal and retrosplenial cortical lesions on habituation, reaction to spatial and non-spatial changes during object exploration in the rat. *Neurobiology of Learning and Memory, 82*, 1-11.

Pearce, J. M., Graham, M., Good, M. A., Jones, P. M., & McGregor, A. (2006). Potentiation, overshadowing, and blocking of spatial learning based on the shape of the environment. *Journal of Experimental Psychology: Animal Behavior Processes, 32*(3), 201-214.

Pearce, J. M., Roberts, A. D. L., & Good, M. (1998). Hippocampal lesions disrupt navigation based on cognitive maps but not heading vectors. *Nature*, *396*, 75-77.

Ratliff, K. R., & Newcombe, N. S. (2008). Reorienting when cues conflict: evidence for an adaptive-combination view. *Psychological Science, 19*, 1301-1307.

Redish, A.D. (1999). *Beyond the cognitive map: From place cells to episodic memory*. The MIT Press.

Rescorla, R. A, & Wagner, AR. (1972). A theory of Pavlovian conditioning: variations in the effectiveness of reinforcement and non-reinforcement. In AH. Black & W.F. Prokasy (eds.), Classical conditioning II: current research and theory (pp. 64-99) New York: Appleton-Century-Crofts.

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

Siegel, A. W., & White, S. H. (1975). The development of spatial representations of large-scale environments. In H. W. Reese (Ed.), *Advances in child development and behavior* (Vol. 10, 9-55). New York: Academic Press.

Spetch, M. L. (1995). Overshadowing in landmark learning: Touch-screen studies with pigeons and humans. *Journal of Experimental Psychology: Animal Behavior Processes, 21*, 166-181.

Spetch, M. L., Cheng, K., & MacDonald, S. E. (1996). Learning the configuration of a landmark array, I: Touch screen studies with pigeons and humans. *Journal of Comparative Psychology, 110*, 55-68.

Spetch, M. L., Cheng, K., MacDonald, S.E., Linkenhoker, B. A., Kelly, D. M., & Doerkson, S. R. (1997). Use of landmark configuration in pigeons and humans: II. Generality across search tasks. *Journal of Comparative Psychology, 111*, 14-24.

Solstad, T., Boccara, C. N., Kropff, E., Moser, M. B., & Moser, E. I. (2008). Representation of geometric borders in the entorhinal cortex. *Science, 322*(5909), 1865-1868.

Teng, E., & Squire, L. R. (1999). Memory for places learned long ago is intact after hippocampal damage. *Nature*, *400*, 675-677.

Thorndyke, P. W., & Hayes-Roth, B. (1982). Differences in spatial knowledge acquired from maps and navigation. *Cognitive Psychology*, *14*, 560-589.

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

Tolman, E. C., & Honzik, C. H. (1930). "Insight" in rats. University of California, Publications in Psychology, 4, 215-232.

Tolman, E. C., Ritchie, B. F., & Kalish, D. (1946). Studies in spatial learning II: Place learning versus response learning. *Journal of Experimental Psychology*, *36*(3), 221-229.

Vass, L. K. & Epstein, R. A. (2013). Abstract representations of location and facing direction in the human brain. *Journal of Neuroscience*, *33*(14), 6133-6142.

White, N. M., & McDonald, R. J. (2002). Multiple parallel memory systems in the brain of the rat. *Neurobiology of Learning and Memory, 77*(2), 125-184.

Wilson, P. N., & Alexander, T. (2008). Blocking of spatial learning between enclosure geometry and a local landmark. *Journal of Experimental Psychology: Learning Memory and Cognition, 34*(6), 1369-1376.

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

Wolbers, T., & Büchel, C. (2005). Dissociable retrosplenical and hippocampal contributions to successful formation of survey representations. *The Journal of Neuroscience*, *25*(13), 3333-3340.

Zhou, R., & Mou, W. (2016). Superior cognitive mapping through single landmark-related learning than through boundary-related learning. *Journal of Experimental Psychology: Learning, Memory and Cognition*. In press.