Developing global spatial memory by navigation in multiscale environments

by

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Abstract

Spatial navigation updates people's self-location (heading and position) and meanwhile develops spatial memory. Environments in real life are often multiscale environments, which contain a number of individual spaces separated by boundaries. People primarily rely on visual cues (piloting) to develop local representations for individual spaces and rely on self-motion cues (path integration) to develop global representations for spatial relations between locations in different individual spaces. Previous studies have shown difficulty in updating self-location globally and developing global representations (e.g., Lei, Mou, & Zhang, 2020; Lei & Mou, under review; Marchette, Marchette, Vass, Ryan, & Epstein, 2014). In the current dissertation, two studies were conducted using immersive virtual reality to investigate the function of across-boundary navigation in developing global representations.

The study in Chapter 2 examined the development of global representations after one-shot across-boundary walking between two square rooms. There were six experiments in this study, which manipulated factors that might affect the encoding and retrieval of global spatial relations. Yet, regardless of these manipulations, all the six experiments showed that the participants updated their headings based on global relations between the rooms. These results in Chapter 2 demonstrated that people can update their self-location globally and develop global representations after one-shot across-boundary walking between two rooms. The encoding and retrieval of global representations developed by path integration may be automatic.

The study in Chapter 3 examined the influence of visual structural similarity in developing global representations after one-shot across-boundary walking. The two rooms in this study were rectangular but were globally misaligned so that updating self-location relative to local structures would conflict with updating self-location relative to global relations. The results from three experiments showed that the participants only updated their self-location locally, however, updating self-location globally could occur if the global representations were successfully activated. These results in Chapter 3 demonstrated that local structural similarity interferes with developing global representations and updating self-location globally, and this interference occurs during activation of global representations.

Overall, the current dissertation has provided evidence that path integration develops global representations after one-shot walking across boundaries in a novel multiscale environment with two rooms, but the visual similarity of structures in local spaces exerts strong interference in this process.

Preface

This thesis is an original work by Xuehui Lei. The experiments in this thesis received research ethics approval from the University of Alberta Research Ethics Board, Project Name "Human navigation in across-boundary and 3 dimensional spaces", No. Pro00082900, July 26, 2019.

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Table of Contents

List of Figures

List of Tables

Chapter 1 General Introduction

In real-life navigation, people move in complex environments that are often not with a single scale but rather with multiple scales. For example, a bedroom is located in a house, a house is located in a neighborhood, and a neighborhood is located in a city. These multiscale environments are usually separated into local spaces by boundaries (e.g., a house separated into different rooms by walls). Through navigational experience, people can develop spatial representations in a multiscale environment. By navigating in local spaces, people can develop local representations for spatial relations in the local spaces. By navigating between local spaces across boundaries, people can develop global representations for spatial relations between locations in different local spaces that are mutually nonvisible (e.g., two locations in different rooms of a house).

Previous studies have well examined whether and how people develop local spatial representations in an immediate local space (Easton & Sholl, 1995; Kelly & McNamara, 2010; Meilinger, Strickrodt, & Bülthoff, 2016; Mou & McNamara, 2002; Sargent, Dopkins, Philbeck, & Chichka, 2010). By contrast, studies on multiscale environments have shown difficulty in developing global spatial representations (Lei, Zhang, & Mou, 2020; Marchette, Ryan, & Epstein, 2017; Marchette, Vass, Ryan, & Epstein, 2014; Wang & Brockmole, 2003). The aim of the current dissertation is to investigate how global spatial relations are encoded by across-boundary navigation in multiscale environments and identify the factors that contribute to the difficulty in this process. The quest to understanding the development of global spatial representations would allow us to recognize the mechanisms and capabilities of across-boundary navigation in spatial memory.

1.1 Self-localization and spatial memory

Spatial navigation is a process in which navigators select routes to move to destinations and meanwhile gather environmental information during movement. During navigation, navigators may explore an environment and update their self-location at different locations in the environment (i.e., identifying their current headings and positions). Meanwhile, navigators also develop spatial representations of heading and position relations between different locations in the environment, which is the idea of cognitive map proposed by Tolman (1948). Updating self-location and developing spatial memory occur simultaneously and they mutually support each other. On one hand, spatial memory is formed with the spatial relations between different locations in the environment and these spatial relations are acquired by self-localization in navigation. On the other hand, spatial memory can facilitate accurate self-localization and can guide navigation efficiently (e.g., choosing a shortcut route). Therefore, spatial navigation leads to the updating of self-location and the development of spatial memory.

Behavioral and neurophysiological studies on humans and non-human animals have provided substantial empirical and theoretical evidence for mechanisms of self-localization and spatial memory. These mechanisms obtained from mobile species have important applications in the field of mobile robotics to solve the problem of simultaneous localization and mapping. Biologically inspired robotics are developed to construct spatial memories and execute self-localization simultaneously in novel environments before robots can be used in domestic homes and workplace (Milford & Wyeth, 2008, 2010).

1.1.1 Mechanisms of self-localization

Previous studies on humans and non-human animals have revealed two methods underlying the updating of self-location and the development of spatial memory, which are path integration and piloting.

Path integration relies on self-motion cues to encode spatial relations between locations on a traversed path. These self-motion cues include optic flow and body-based cues such as proprioceptive information, vestibular information and motor efference copy (Etienne & Jeffery, 2004; Gallistal, 1990; Klatzky, Loomis, Beall, Chance, & Golledge, 1998; Loomis, Klatzky, Golledge, & Philbeck, 1999; Rieser, Guth, & Hill, 1986; Tcheang, Bulthoff, & Burgess, 2011; Wang, 2017; Warren, Kay, Zosh, & Sahuc, 2001; see Rieser, 1999 for a review). Path integration keeps track of navigators' moving speeds and directions to calculate the Euclidian spatial relations between locations on a circuitous path and to continually update navigators' self-location (Mittelstaedt & Mittelstaedt, 1980; Müller & Wehner, 1988; Wang, 2016). Empirical studies have shown that when locomoting in a local space without vision, people can update their self-location and also self-to-object vectors based on self-motion (Klatzky, et al., 1990; Rieser, 1989; Wang & Spelke, 2000). Studies using non-human animals have also shown that in natural environments without visual features, desert ants can use path integration to return to the home and previously visited food sources (Collett, Collett, & Wehner, 1999; Etienne et al., 1998; von Frisch, 1967).

By contrast, piloting relies on perception, primarily vision, to encode spatial relations between locations. Navigators can directly see the spatial relations between visible locations as well as the spatial relations between themselves and other locations (Cheng & Spetch; 1998). Studies have shown that people who are disoriented to have path integration disrupted, can use visual cues (e.g., familiar landmark cues or a boundary) to determine self-location as well as other goal locations (Doeller & Burgess, 2008; Etienne, Maurer, Boulens, Levy, & Rowe, 2004; Foo, Warren, Duchon, & Tarr, 2005; Nardini, Jones, Bedford, & Braddick, 2008; Wehner, Michel, & Antonsen, 1996). In addition, non-human animals can also use visual cues to reorient themselves in an environment (Cheng, 1986; Cheng & Spetch, 1998). For example, in insects (e.g., honeybees and ants), sun compass and the polarization pattern of the sky can indicate directional information (Wehner and Müller, 2006).

Therefore, humans and non-human animals can update self-location and develop spatial memory by path integration and piloting. These two methods can function independently and also complement each other. Path integration can provide metric information in a spatial framework to incorporate landmarks (Savelli & Knierim, 2019). Spatial memory acquired by piloting may also provide an internal reference system to facilitate path integration even when the piloting cues are no longer available (Arthur, Philbeck, & Chichka, 2007; Kelly, Avraamides, & Loomis, 2007; Philbeck & O'Leary, 2005). Furthermore, since path integration is error-prone, piloting can intermittently remove the accumulated errors and reset path integration (Etienne et al., 2004; Foo et al., 2005; Kelly et al., 2007; Mou & Zhang, 2014; Zhang & Mou, 2017; Zhao & Warren, 2015a, 2015b).

1.1.2 Neural basis for self-localization

In recent decades, the neural encoding of spatial locations and orientations has been identified in mammalian brains. The vast majority of the findings are benefited from single-unit recordings which involve rats freely navigating in an environment with electrode recordings. The studies on humans mostly rely on virtual reality to simulate navigation and use neuroimaging on healthy humans.

To encode spatial properties of locations, orientations and metrics, there are three fundamental types of spatial cells. Place cells in the hippocampus, which fire in a certain region of an environment, provide coding for location information (O'Keefe & Dostrovsky, 1971). Place cell firing patterns (firing rate and firing location) are specific to environments and the patterns change in different environments, which is a process known as remapping (Anderson & Jeffery, 2003). The second type of spatial cells is heading direction cells in the entorhinal cortex, subiculum, and retrosplenial cortex. Heading direction cells increase firing rate for certain facing directions to signal orientation information (Ranck, 1984). Across different environments, the absolute preferred firing direction of a heading direction cell is different; however, the offset between preferred firing directions of heading directions cells remains the same, which means the cells that share the same preferred firing direction in one environment will still fire at the same time in another environment (Yoganarasimha, Yu, & Knierim, 2006). The third type of spatial cells is grid cells in the medial entorhinal cortex. Grid cells exhibit multiple firing fields in an environment and the regularity of firing fields forms a hexagonal grid-like array (Fyhn, Molden, Witter, Moser, & Moser, 2004; Hafting, Fyhn, Molden, Moser, & Moser, 2005). The spatial periodicity of grid cells allows to measure the distance between locations. Grid cells cluster into several modules, with the cells from the same module maintaining the relative position of firing fields and different modules independently responding to the change of environments (Stensola et al., 2012). Since the offset in preferred firing directions of head direction cells and the spatial relationship in firing fields of grid cells can remain constant across environments, these cells may provide a general metric representation of space (Fyhn et al., 2004; Moser & Moser, 2008; but see Krupic, Bauza, Burton, Barry, & O'Keefe, 2015).

Self-motion cues in path integration and perceptual cues (e.g., visual or olfactory cues) in piloting can independently or jointly influence the firing patterns of place cells, head direction cells and grid cells. For example, place cells and grid cells of rats can fire in darkness by using self-motion cues alone (Hafting et al., 2005; Terrazas et al., 2005), and environmental geometry and distal landmarks can respectively affect grid cell symmetry and place cell firing field (Krupic et al., 2015; Renaudineau, Poucet, & Save, 2007). Head direction cells of flies can maintain directional tuning based on visual landmarks when available as well as self-motion cues in darkness (Seelig & Jayaraman, 2015). The activity in the spatial cells can also be determined by a combination of different cues in path integration and piloting. Studies testing mice in virtual reality have shown that visual information and self-motion are combined nonlinearly to determine place cell firing locations (Chen, King, Burgess, & O'Keefe, 2012). In addition, visual cues of environmental features can fine-tune the computation in path integration and correct cumulative errors in path integration, which is evident in place cell firing patterns (Jayakumar et al., 2019).

1.2 Self-localization and spatial memory in multiscale environments

People live in multiscale environments (Han & Becker, 2014). A multiscale environment (an environmental space, namely, a space containing several vista spaces, Montello, 1993) is usually separated into individual spaces (a vista space, namely, an immediate visible surrounding, Montello, 1993) by boundaries. In some multiscale environments, local spaces share similar structures/layouts. For example, in a campus building, the classroom interiors may be visually similar in terms of geometries and features. In multiscale environments, spatial relations in local scales involve relations of distances and directions between locations in immediate local spaces, and spatial relations in global scales involve relations of distances and directions between locations that are in different local spaces across boundaries. People can update their self-location and develop spatial representations in both local and global scales (Lei et al., 2020; Lei & Mou, under review; Shine, Valdés-Herrera, Hegarty, & Wolbers, 2016).

1.2.1 Local self-localization and spatial memory

In multiscale environments, people primarily encode local spatial representations that can be generalized into geometrically similar local spaces (Marchette et al., 2017; Marchette et al., 2014; Wang & Brockmole, 2003). In Marchette et al. (2017), the participants learned objects' locations in four structurally similar but visually distinct buildings, and then they were tested to replace the objects at the remembered locations. The results showed frequent errors in confusions of geometrically equivalent locations in different buildings (e.g., at a locally correct corner but in a wrong building), indicating that the participants have primarily formed schematic representations of local spaces rather than the identity and locations of local spaces in the global environment. Furthermore, the geometric confusions were not limited to local spaces with metrically identical geometries but were also observed in local spaces with different geometries as long as geometrical equivalence could be defined.

Some neurophysiological studies have also provided evidence for local spatial representations in multiscale environments. When rats freely foraged in an environment which contained multiple visually identical compartments, place cell firing fields exhibited spatial repetition across compartments even after the extensive navigational experience, suggesting that place cells provided local coding of a multiscale environment (Spiers, Hayman, Jovalekic, Marozzi, & Jeffery, 2015). Similarly, Derdikman et al. (2009) recorded place cells and grid cells when rats ran through an environment comprising multiple identical tracks and showed that maps of place cells and grid cells were fragmented into repeating submaps. This field repetition may be caused by the resetting of firing fields when the rats ran through the turning point between local spaces (e.g., doorway of a compartment). These results suggest that when rats navigate between local spaces in a multiscale environment, visual cues of similar local structures exert a strong influence on the locations of place fields and grid fields to update the rats' self-location locally; path integration is reset by visual cues when the rats enter a local space that is structurally similar as a previous local space.

This phenomenon of resetting by visual structural similarity is demonstrated in human behavioral studies as well. In Riecke and McNamara (2017), the participants learned objects' locations in one room, and then they were disoriented to walk into another room that shared a similar geometry with the learning room. When tested to mentally adopt perspectives in the remote learning room, the participants performed better when the imagined perspective in the learning room and their current physical perspective in the testing room were locally aligned (e.g., both physical and imagined perspectives were facing doorways of the rooms) rather than misaligned, suggesting that the participants updated their self-location based on visual structural similarity in immediate and remote spaces. This visual-based updating is based on local representations.

Therefore, when navigating in a multiscale environment with several local spaces, people can update their self-location with respect to the visual similarity of structures in local spaces and develop local spatial representations that are generalized to geometrically similar local spaces. Piloting (visual cues) is the primary mechanism to update self-location locally and develop local representations.

1.2.2 Global self-localization and spatial memory

In multiscale environments, due to the existence of boundaries between local spaces, people in one space cannot directly see locations in another space. Thus, people cannot directly perceive the global relations between locations in different local spaces by piloting. Instead, they may primarily rely on path integration in across-boundary navigation to encode global relations. Some researchers believe that path integration can support self-localization and spatial learning in large-scale environments (Gallistel, 1990; Gallistel & Matzel, 2013; Hübner & Mallot, 2007; Jacobs & Schenk, 2003; Loomis et al., 1999; McNaughton, Battaglia, Jensen, Moser, & Moser, 2006; Meilinger, 2008; Milford & Wyeth, 2008). However, empirical studies have shown mixed findings regarding the existence of global spatial representations in multiscale environments.

Some studies have demonstrated the inexistence of global representations (Marchette, et al., 2017; Marchette et al., 2014; Radvansky & Copeland, 2006; Spiers et al., 2015; Wang & Brockmole, 2003). For example, Wang & Brockmole (2003) reported that the participants could not point to another building on campus if they were standing within one building but they could do so when going outside the building, indicating that the participants might not have global representations of locations with the building in terms of the campus. Some other studies have revealed the existence of global spatial representations, but with some prerequisites such as some prior global learning of the environment before learning local spaces (Lei & Mou, under review; Lei et al., 2020;) and explicit instructions to encode global spatial information for local views (Shine et al., 2016).

Furthermore, even after developing global spatial representations by prior global learning and extensive navigational experience in multiscale environments, people may still only rely on local representations, rather than global representations, to update their self-location during navigation (Lei & Mou, under review). Only when the global representations in long-term memory are activated by global-relevant tasks to be on the sensorimotor level in working memory, can people update self-location in global representations. This suggests the difficulty in using global representations to update self-location.

Mixed findings have also been shown from neural evidence regarding whether place cells and grid cells can form coherent global patterns to support global representations. Some neuroscientific studies have provided evidence for spatial representations in global scales in addition to local scales. Studies on rats using a large enclosure have revealed that the spacing and sizes of grid and place firing fields can represent spatial relations in different spatial scales (Hafting et al., 2005; Kjelstrup et al., 2008), and the ventral-to-dorsal axis of hippocampus supports a gradient of representational scales (Strange, Witter, Lein, & Moser, 2014). When testing rats in an environment with two connected compartments where local and global directions conflicted, the head direction cells in the dysgranular retrosplenial cortex could have a sub-population being controlled only by local landmarks and another sub-population showing bi-directional tuning to both local landmarks and global directions (Jacob et al., 2017). Regarding humans, Brunec and colleagues (2018) tested participants in well-known large-scale environments without boundary-crossing and showed that human anteroposterior hippocampus provides coarse-to-fine spatial representations.

However, these evidence are based on navigation in local space or an environment without boundary-crossing. When recording in multiscale environments containing several across-boundary compartments, some studies showed that place cells and grid cells showed purely local coding but no global coding (Derdikman et al., 2009; Spiers et al., 2015) while some other studies showed the influence of navigational experience on this issue. In Carpenter, Manson, Jeffery, Burgess and Barry (2015), during initial exposures to a two-compartment environment, grid cell firing patterns were dominated by local environmental cues and replicated between compartments; yet, with prolonged experience, grid cell firing patterns formed a single, continuous representation that spanned both compartments. This indicates that extensive navigational experience may play a role in developing global representations.

Therefore, when navigating across local spaces in a multiscale environment, under some conditions, people can develop global representations for spatial relations across boundaries and update their self-location globally. Path integration in across-boundary navigation is the primary mechanism to update self-location globally and develop global representations.

1.3 Difficulty in global self-localization and spatial memory

Based on the aforementioned studies, when navigating in multiscale spaces, local self-localization, which is primarily supported by visual cues of local spaces (piloting), functions smoothly with no difficulty. By contrast, global self-localization, which is primarily supported by self-motion cues in across-boundary navigation (path integration), functions with difficulty and requires preconditions. There are some possible factors that contribute to the difficulty in updating self-location globally and developing global representations reported in the previous studies.

First, the lack of global representations may be due to the noisy nature of path integration. The characteristic of path integration is that errors are quickly accumulated over time along complicated paths (Etienne & Jeffery, 2004; Souman, Frissen, Sreenivasa, & Ernst, 2009; Zhao & Warren, 2015a) and visual cues of geometry or landmarks are needed to correct the errors (Kelly, McNamara, Bodenheimer, Carr, & Rieser, 2008; Knaden & Wehner, 2006). Since multiscale environments contain boundaries to block views across local spaces, the function of piloting to correct path integration is undermined. Thus, an accurate global self-location and representation may be hard to develop by path integration per se.

Second, the existence of boundaries in multiscale environments is also worth consideration. Previous studies have suggested that boundaries can influence the organization of spatial memory. Spatial memory may be generally fragmented with spatial knowledge organized by regions, and spatial relations between regions may be less accurately represented compared with within-region spatial relations (e.g., Brockmole & Wang, 2003; McNamara, 1986; Wang & Brockmole, 2003). Retrieving spatial and event information in one space is impaired when people move to a new location in an adjacent space across boundaries compared to when they move to a new location within the same space (Radvansky & Copeland, 2006; Radvansky, Tamplin, & Krawietz, 2010). In addition, neurological studies have revealed that environmental boundaries strongly influence spatial coding of grid cells and place cells (Derdikman et al., 2009; Krupic et al., 2015; Lever, Burton, Jeewajee, O'Keefe, & Burgess, 2009; Spiers et al., 2015), and the clustering of place field edges near boundaries may be the reason why environmental boundaries distort mental representations of physical spaces (Wang, Monaco, & Knierim, 2020). Thus, boundaries may impair encoding global relations by navigation across boundaries.

Nevertheless, there are other studies showing that boundaries may not play a role. Mou and Wang (2015) showed that the performances to point to objects' original locations were comparable when the participants walked a path within the same room or across rooms, which demonstrated that boundaries do not impair path integration to encode global relations. Thus, people may update self-location relative to global relations after one-shot across-boundary navigation equally well when moving either between rooms or within the same room.

Third, human spatial memory may be primarily concerned with local spatial relations and secondarily concerned with global relations. Since people actively interact with immediate surroundings to avoid obstacles in navigation and execute actions to reach goals, spatial information in the immediate local space are represented in sensorimotor representations in working memory to get ready for motion. Thus, updating self-location relative to local boundaries or local features may be prioritized during navigation. Contrarily, global relations with remote local spaces are not directly relevant to navigation in immediate surroundings, and global self-localization may not be attended to. Explicit instructions to encode global relations (Shine et al., 2016) and global-relevant tasks (Lei & Mou, under review) may draw attention to global relations so that sensorimotor representations can be based on global representations. These sensorimotor global representations are then updated in navigation and as a result, people update self-location globally and develop global representations.

Fourth, some previous studies demonstrating difficulty in updating global self-location have used virtual environments without full-body movement, thereby may have suffered from the lack of full body-based cues in path integration (Han & Becker, 2014; Lei et al., 2020; Marchette et al., 2017; Marchette et al., 2014). Some of these studies have used desktop virtual environments which did not provide any physical movement but only visual translation and visual rotation (Han & Becker, 2014; Marchette et al., 2017; Marchette et al., 2014). Some other studies have used immersive virtual environments which allowed physical rotation but still visual translation instead of physical translation (Lei & Mou, under review; Lei et al., 2020; Shine et al., 2016). The importance of physical rotation and translation in path integration and in developing global representations of large-scale environments has been demonstrated in previous studies (Chance, Gaunet, Beall, & Loomis, 1998; Klatzky et al., 1998; Rieser, 1989; Ruddle, Volkova, & Bülthoff, 2011; Taube, Valerio, & Yoder, 2013; Waller, Loomis, & Haun, 2004). The lack of full-body movement in virtual reality may limit the function of path integration to update self-location globally and develop global representations by across-boundary navigation.

The error-prone nature of path integration, the existence of boundaries, the priority of local relations in human spatial memory, and the lack of body-based cues in navigation may coexist to impair updating global self-location and developing global spatial memory in multiscale environments. The prerequisites to develop global representations, such as extensive across-boundary navigation experience, some prior global learning, and explicit instructions to encode global relations (Carpenter et al., 2015; Lei & Mou, under review; Lei et al., 2020; Shine et al., 2016) may help cope with these factors. For example, some prior global learning, which is spatial learning of some other entities in the global environment prior to learning local spaces, may provide a global frame to scaffold subsequent learning of new spatial information at new perspectives in local spaces (Kelly & McNamara, 2010; Philbeck & O'Leary, 2005). This prior learning of the global environment may facilitate path integration to integrate spatial knowledge across local spaces and may help reduce the possible impairment from boundaries.

1.4 Thesis outline

The primary research goal of my dissertation is to investigate the function of across-boundary navigation to update self-location globally and develop global representations in multiscale environments and to examine possible reasons leading to the difficulty in this process. Previous studies on global representations in multiscale environments have focused on global spatial memory after the extensive navigational experience (Lei et al., 2020; Marchette et al., 2017; Marchette et al., 2014; Shine et al., 2016). To better understand the function of path integration and the relationship between spatial navigation and spatial memory, the current dissertation focuses on one-shot across-boundary navigation in novel multiscale environments. In addition, the current dissertation enables physical walking, which means the participants have full-body movement during navigation, to make the experiments more ecological as real-life scenarios and to better examine the function of path integration. Therefore, the current dissertation tests the function of one-shot across-boundary walking in updating self-location globally and developing global representations in novel multiscale environments.

To reflect the updated self-location in local and global representations, sensorimotor alignment effect is examined in a judgment of relative direction (JRD) task. In the JRD task, participants, while facing a physical perspective in the current local space, are asked to mentally adopt an imagined perspective in another remote local space and then point to a target. The sensorimotor alignment effect refers to better performances when the physical perspective in the current space and the imagined perspective in the remote space are aligned rather than misaligned (Kelly et al., 2007; Riecke & McNamara, 2017; Shelton & Marchette, 2010). If the alignment between the physical and imagined perspectives is based on local/global relations (e.g., local alignment means that both perspectives are facing the doors of local spaces, and global alignment means that both perspectives are facing north), then a local/global sensorimotor alignment effect will reflect the updated headings in local/global representations.

Chapter 2 investigates the development of global spatial representations from one-shot across-boundary walking and the impairing role of boundaries in path integration. The participants first learned some objects in a square room and then they were blindfolded and led to walk a path to a novel square room for testing. During testing, while they were facing different physical perspectives in the testing room, they conducted the JRD task which asked them to adopt imagined perspectives in the learning room indicated by the learned objects and point to the direction of a target object. If the participants updated their headings relative to global relations between the two rooms, then there would be a global sensorimotor alignment effect.

In Chapter 2, Experiment 1 manipulated the existence of boundaries. The participants walked from the learning location to the testing location either across boundaries or within the same boundaries. The results showed comparable global sensorimotor alignment effects from across- or within-boundary walking, indicating no impairment from boundaries. Experiments 2-6 centered on across-boundary walking and constantly showed global sensorimotor alignment effects after manipulating factors related to encoding global relations in walking and retrieval of global relations in the JRD task. These results indicate that people update self-location globally and develop global representations after one-shot across-boundary walking.

Chapter 3 examines whether the visual similarity of local structures interferes with updating self-location globally. As mentioned in the previous section, studies have proposed some possible reasons for the reported difficulty in developing global representations of multiscale environments. However, one key possibility that has been overlooked is the structural similarity of local spaces. The visual similarity of local structures can update self-location relative to local boundaries and local features after across-boundary navigation (Derdikman et al., 2009; Riecke & McNamara, 2017; Spiers et al., 2015). This local structural similarity that is misaligned with global relations may impair updating self-location globally.

To make the structural similarity of local spaces valid to determine self-location, the study of Chapter 3 used two rectangular rooms with a window on one short wall. To differentiate local and global self-localization, the two rooms were globally misaligned (i.e., one north-south oriented, the other one east-west oriented). However, the result of Experiment 1 showed only local but no global sensorimotor alignment effects, indicating that the participants only updated their self-location locally. This is opposite to the robust findings of global sensorimotor alignment effects in Chapter 2. Experiments 2 and 3 then tested whether activating global representations prior to the JRD task could lead to updating self-location globally. The participants did a task to judge global heading relations between the two rooms (Burte & Hegarty, 2004; Lei & Mou, under review; Sholl, Kenny, & DellaPorta, 2006) while seeing the testing room (Experiment 2) or in darkness (Experiment 3). Experiment 2 only showed the local sensorimotor alignment effect but Experiment 3 showed both global and local sensorimotor alignment effects. These results demonstrate that visual similarity of local structures can interfere with updating global self-location and developing global representations. This interference occurs in activating global representations. After successful activation, the local structural similarity does not impair updating global self-location and developing global representations.

In Chapter 4, the main findings of the studies are summarized. The implications for the function of path integration, the interaction between piloting and path integration, and the relationship between across-boundary navigation and multiscale spatial memory are discussed. Furthermore, possible future studies are suggested.

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Chapter 2 Developing Global Spatial Memories by One-Shot Across-Boundary Navigation

2.1 Abstract

This study investigated to what extent people can develop global spatial representations through one-shot across-boundary walking in a novel environment. In Experiment 1, the participants learned objects' locations in one room. Then, they were blindfolded and led to walk to a new position either within the room or in a novel room. They did a judgment of relative direction task in which they adopted imagined perspectives determined by the remembered locations of objects and pointed to relative directions of the remembered locations of target objects. The results showed comparable sensorimotor alignment effects (i.e., better performances from the imagined perspectives aligned with participants' physical perspectives than from the misaligned imagined perspectives) for both within- and across-boundary walking conditions. Experiments 2-6 focused on across-boundary walking. Experiments 2-3 tested factors related to encoding global relations (i.e., explicit instructions to attend to walking and keep track of spatial relations, and visual cues for navigational affordance to another space). Experiments 4-6 tested factors of task trials that might be related to retrieving global relations in the task (i.e., learning orientation as one imagined perspective, learning position and orientation as the imagined viewpoint, and the number of imagined perspectives). The results still showed sensorimotor alignment effects after manipulating these factors. These results indicate that people update self-location relative to a global environment including two rooms and develop global spatial memories by one-shot walking.

Keywords*:* sensorimotor alignment effect; spatial memory; path integration; boundary; navigation

2.2 Introduction

In daily life, it is common for people to navigate between spaces that are separated by boundaries (e.g., moving between two rooms at home). Understanding whether and how people develop global spatial memory of across-boundary spaces by navigation is theoretically important (Mou & Wang, 2015; Wang & Brockmole, 2003). Recent studies have demonstrated that people can develop global representations of spatial relations between across-boundary locations (encoding the relative orientations of two rooms) through extensive across-boundary navigation (e.g., Lei, Mou, & Zhang, 2020; Shine, Valdés-Herrera, Hegarty, & Wolbers, 2016; Strickrodt, Bülthoff, & Meilinger, 2019). The current study aims to examine the development of global spatial representations after one-shot across-boundary navigation between spaces in a novel environment.

Understanding spatial memory acquired from across-boundary navigation is critical to understanding the specific roles of different navigation methods in developing spatial memory. In navigation, people primarily rely on two methods to update self-location (their positions and headings) and develop spatial memories. One method is path integration, in which people rely on self-motion cues (including optic flow and idiothetic cues) to continually update their self-location (Etienne & Jeffery, 2004; Etienne et al., 1998; Loomis, Klatzky, Golledge, & Philbeck, 1999; Mittelstaedt & Mittelstaedt, 1980). The other method is piloting, in which people rely on perceived landmarks to update their self-location (Etienne, Maurer, Boulens, Levy, & Rowe, 2004; Foo, Warren, Duchon, & Tarr, 2005; Wehner, Michel, & Antonsen, 1996). These two methods complement each other. Path integration can provide a metric for a spatial framework to organize landmarks (Savelli & Knierim, 2019), whereas piloting can correct, recalibrate, and also reset path integration (Etienne et al., 2004; Jayakumar et al., 2019; Zhang & Mou, 2017).

However, the exact role of path integration in developing global spatial memory is controversial in the literature. Some researchers conjecture that when piloting cues are minimal, path integration plays a critical role in developing spatial memory. In a large-scale environment, people in one space may not visually see another space. People primarily rely on path integration to encode global spatial relations between these two spaces and then integrate locations of objects in these two spaces in global spatial representations (Gallistel, 1990; Gallistel & Matzel, 2013; Jacobs & Schenk, 2003; Lei et al., 2020; Loomis et al., 1999; McNaughton, Battaglia, Jensen, Moser, & Moser, 2006; Meilinger, 2008). In contrast, other researchers de-emphasize the function of path integration in developing global spatial representations (e.g., Wang, 2016; Warren, Rothman, Schnapp, & Ericson, 2017). There are two major reasons why people may not be able to develop spatial memories only based on path integration, especially in a large-scale environment. First, path integration is error-prone, and errors in path integration are rapidly accumulated after walking complex paths in a large-scale environment. Second, path integration is primarily engaged with the local immediate space and does not keep track of self-location relative to a remote space (Wang, 2004; Wang & Brockmole, 2003). Thus, path integration may not be able to develop global spatial representations.

To differentiate between these theoretical arguments, researchers have examined the development of global spatial memories from across-boundary navigation, which provides a strict test of the role of path integration in developing global spatial memories (e.g., Lei et al., 2020; Marchette, Vass, Ryan, & Epstein, 2014; Wang & Brockmole, 2003). In across-boundary spaces, researchers can minimize the influence of piloting because participants cannot directly see spatial relations between locations in two spaces separated by boundaries. Therefore, whether participants develop representations of spatial relations across boundaries or not strictly tests the pure role of path integration in developing global spatial memories. Recent studies have shown that in some restricted experimental situations, participants can develop global memories of spatial relations between across-boundary locations by across-boundary navigation (e.g., Lei et al., 2020; Shine et al., 2016). In their studies, the participants navigated along a simple path. They also had extensive experiences of navigating between across-boundary spaces. In addition, in Shine et al. (2016), the participants were explicitly instructed to learn the across-boundary spatial relations (orientations in one room relative to global landmarks outside). In Lei et al. (2020), the participants could not develop global representations for spatial relations between rooms unless they had learned the environment outside the rooms before learning objects' locations in the rooms. The precondition of using a simple path is not surprising because it is well known that path integration is error-prone (Kelly, McNamara, Bodenheimer, Carr, & Rieser, 2008; Wang & Brockmole, 2003). In contrast, the precondition of extensive navigation experiences seems less clear given the inconsistent findings in the literature.

Some previous studies show that navigation experiences during learning may play a role in developing global memories in large-scale environments (Han & Becker, 2014; He, McNamara, Bodenheimer, & Klippel, 2019; Starrett, Stokes, Huffman, Ferrer, & Ekstrom, 2019). In Han and Becker (2014), when given more learning time in a novel environment containing two neighbourhoods, the participants developed integrated representations of the two neighbourhoods, whereas when given fewer learning trials, they developed separate representations of the two neighbourhoods. Starrett et al. (2019) also showed that the use of boundaries to anchor global representations emerged as learning experiences increased in a novel environment (see also He et al., 2019 for better spatial knowledge acquisition over time in route learning and survey learning). However, other studies have shown that navigation experiences do not affect developing global memories. Ishikawa and Montello (2006; see also Weisberg, Schinazi, Newcombe, Shipley, & Epstein, 2014) demonstrated that there are individual differences in integrating and developing configural knowledge, with some participants improving and others remaining the same (either being accurate from the beginning or being inaccurate until the end) over learning sessions. Thus, the role of extensive navigation experiences in developing global memories in large-scale environments is not clear. Similarly, the navigation experiences may or may not affect the development of global spatial representations by across-boundary navigation reported by the previous studies (Lei et al., 2020; Shine et al., 2016).

It is important to investigate whether the development of global spatial representations occurs after one-shot across-boundary navigation (e.g., after one walks from one room to the neighbouring room for the first time). If the development of global spatial memories after one-shot across-boundary navigation occurs, then this result will strongly support the theoretical position that people primarily rely on path integration to encode global spatial relations and develop global spatial representations (Gallistel, 1990; Gallistel & Matzel, 2013; Jacobs & Schenk, 2003; Lei et al., 2020; Loomis et al., 1999; McNaughton et al., 2006; Meilinger, 2008). If one-shot across-boundary navigation cannot lead to global spatial representations, but extensive across-boundary navigation can (Lei et al., 2020; Shine et al., 2016), then it suggests that only primitive global spatial representations are developed in earlier navigation, and these primitive global spatial representations might support later navigation. Mature global spatial representations are formed as a result of such a reciprocal relationship between navigation and spatial memory. Therefore, examining the development of global spatial representations after one-shot across-boundary navigation can provide insight into the relationship between spatial memory and navigation.

To the best of our knowledge, Kelly, Avraamides, and Loomis (2007) conducted the only study examining the development of global spatial representations after one-shot across-boundary navigation. In their study, the participants learned objects' locations in one virtual room and then physically walked through a virtual wall into another virtual room. The testing room was either visually the same or different from the learning room. In a judgment of relative direction (JRD) task, the participants adopted imagined perspectives in the learning room and pointed to target objects from the imagined perspectives using memories. The global spatial representations between the learning and testing rooms were assessed by a global sensorimotor alignment effect, which showed better performances when the imagined perspective in the learning room and the physical perspective in the testing room were aligned than when the two perspectives were misaligned. A global sensorimotor alignment effect would indicate that people encode their physical perspectives in the testing room and the locations of objects in the learning room in the same global spatial representations. Otherwise, the alignment or misalignment between their physical perspectives in the testing room and imagined perspectives in the learning room should not matter in the JRD task. Note that the JRD task itself does not require any global spatial relations because, in a JRD trial, all objects specifying the imagined perspectives and the targets are in the learning room. Therefore, any global sensorimotor alignment effect should be attributed to global spatial representations that have been formed prior to the JRD task.

Unfortunately, the results of Kelly et al. (2007) were mixed. The global sensorimotor alignment effect occurred when the testing room looked the same as the learning room but did not occur when the testing room looked different from the learning room. These mixed results can be interpreted either to disprove or support the possibility of developing global spatial representations from one-shot across-boundary navigation. On the one hand, the null sensorimotor alignment effect might suggest that people cannot develop global spatial representations from one-shot across-boundary navigation. The global sensorimotor alignment effect when the testing room looked the same as the learning room could be attributed to re-anchoring in the learning room based on visual similarity (Marchette, Ryan, & Epstein, 2017; Marchette et al., 2014; Riecke & McNamara, 2017). Riecke and McNamara (2017) showed sensorimotor alignment effects that were based on the visual similarity between the learning and testing rooms. The participants in their study were disoriented between learning and testing to remove the role of path integration. Inspired by this idea, we speculate that the participants in Kelly et al. (2007) might have re-anchored themselves back to the learning room when they entered the testing room and saw the visually similar room. Therefore, the participants' initial orientation/heading in the updated representations produced by re-anchoring might have been the same as the walking direction from the learning room to the testing room. As the walking direction across rooms was coincidental with the global relation between the two rooms, the participants' initial orientation/heading due to re-anchoring appeared to be the global heading. The participants might then have updated their headings from this initial heading when they turned their bodies, thus producing the global sensorimotor alignment effect. When the testing room looked different, because visual-based re-anchoring did not occur, no global sensorimotor alignment effect was expected.

On the other hand, the result of a global sensorimotor alignment effect suggests that people can develop global spatial representations from one-shot across-boundary navigation. However, these representations may not always be used in the JRD task of imagined perspective-taking, depending on how strong the updated spatial representations are. In long-term memory, people always encode their original learning position and orientation in the learning room (Shelton & Marchette, 2010). We refer to this as original self-localization representations in long-term memory. People can use the original learning orientation in the learning room as the testing orientation when global spatial representations updated by path integration are so weak as to be ignored. Hence, the global sensorimotor alignment effect appears more likely when there are stronger global representations updated by path integration. If we assume that the representations of the global spatial relations are stronger when the learning and testing rooms look the same than when they look different (Han & Becker, 2014), then we can explain the appearance of the global sensorimotor alignment effect in the former but not in the latter.

Therefore, it is still not clear whether the development of global spatial memories from across-boundary navigation reported by the previous studies (Lei et al., 2020; Shine et al., 2016) still occurs for one-shot across-boundary navigation. As Kelly et al. (2007) was the only study tackling this important question and their results were mixed, the primary purpose of the current study was to systematically examine the extent to which the development of global spatial memories occurs by one-shot across-boundary navigation. We conducted experiments to remove the possibility of using visual-based re-anchoring by making the testing room visually different from the learning room. We also increased the likelihood of producing stronger global spatial representations, assuming that people can develop global spatial representations from one-shot across-boundary navigation.

In the current study, we made navigation in the virtual environments more similar to navigation in real environments. The participants in Kelly et al. (2007) walked through a virtual wall into the testing room. In addition, their rooms were octagonal. The unusual movement through walls and unusual shapes of rooms might make the participants perceive the virtual environments differently from the real environments, and they might perform differently from when they are in real-life scenarios (e.g., they may be more likely to ignore spatial updating in virtual environments than in real environments). The current study made the virtual environments and walking between rooms more naturalistic, for example, by superimposing the virtual rooms onto the real rooms, having the participants touch the real environments to calibrate the virtual environments, and having them walk naturally through real doorways towards the neighbouring testing room. In addition, we significantly increased the number of participants in each experiment to increase power. In Kelly et al., 16 participants were used in each experiment. This participant number has a large power to detect a large effect (e.g., power is 0.75 for a Cohen's *d* of 1.0 at the alpha level of 0.05 in a two-tailed *t* test) but not a medium effect (e.g., power is 0.26 for a Cohen's *d* of 0.5 at the alpha level of 0.05 in a two-tailed *t* test). We assume that the sensorimotor alignment effect due to visual-based re-anchoring was large (e.g., Cohen's $d = 1.0$) but that the sensorimotor alignment effect due to global spatial relations updated by path integration was medium (e.g., Cohen's $d = 0.5$). As visual-based re-anchoring might have occurred when the testing and learning rooms looked the same, 16 participants might be enough to detect the sensorimotor alignment effect. However, 16 participants might not be enough to detect the global sensorimotor alignment effect due to the global representations developed by path integration when the testing and learning rooms looked different.

It is worth noting that, in the literature, it is even not clear whether people can update self-location relative to an array of objects across a distance but within the same room after they walk from the learning to testing positions in the same room. The null sensorimotor alignment effect when the learning and testing rooms looked different in Kelly et al. (2007) could just be due to the relatively far distance between the testing position and the objects rather than due to across-boundary walking. In the current study, we also tackle this issue. The participants walked the same distance between the learning and testing locations within the same room or in different rooms. If there was no sensorimotor alignment effect even in the condition of within-boundary navigation, this result would strongly undermine the possibility that global spatial representations could be developed by walking a distance in one-shot navigation whether navigation was within or across boundaries. If there were sensorimotor alignment effects in both within- and across-boundary navigation conditions, the contrast of the sensorimotor alignment effect in the across-boundary condition to the effect in the within-boundary condition could be informative to examine the independent contribution of boundaries in impairing path integration in addition to the navigation distance. Some previous studies have shown that boundaries might not impair path integration (Mou & Wang, 2015), whereas others have suggested that boundaries might significantly impair path integration (Radvansky & Copeland, 2006; Radvansky, Tamplin, & Krawietz, 2010; Wang & Brockmole, 2003). Hence, the second purpose of the current study was to test the impairing role of boundaries in path integration.

There were six experiments in the current study. The design for each experiment is summarized in Table 2.1. Experiment 1 examined whether people update their headings relative to the global environment after one-shot walking across boundaries and whether boundaries play a role in it. Experiments 2-6 only focused on one-shot across-boundary walking. In particular, Experiments 2-3 examined factors that might affect encoding global spatial relations before testing. Experiments 4-6 examined factors in the JRD trial that might affect choosing the updated global self-localization representations or the original self-localization representations in long-term memory in the JRD task.

2.3 Experiment 1

The primary purpose of Experiment 1 was to investigate whether people can update headings in global representations after one-shot walking across boundaries. In addition, Experiment 1 was also designed to test whether the existence of boundaries (independent of the distance between the testing position and the objects) impairs updating headings globally. The participants were divided into two groups, with one group walking across boundaries and the other group walking within the same boundary. As proposed in the introduction of this chapter, if people update headings relative to global relations after one-shot walking, whether walking across boundaries or within a boundary, then the participants would show comparable sensorimotor alignment effects in both across-boundary and within-boundary walking conditions. If people cannot update relative to global relations after one-shot walking of a relatively long distance, then the participants would show no sensorimotor alignment effects regardless of whether they are walking across or within boundaries. If people can update relative to global relations after one-shot walking across boundaries, but boundaries independently impair path integration, then there would be a smaller sensorimotor alignment effect after across-boundary walking than after within-boundary walking.

Table 2. 1 Learning orientation, testing trial types, across-/within-boundary walking, instructions for attention during walking, the door in the virtual learning room, and allocentric/egocentric pointing in the task in all experiments.

Experiment	Learning orientation	Trial type	Boundary	Instruction	Door	Pointing
Exp 1: across boundary	270°	Aligned, Misaligned	Across	Yes	Yes	Allocentric
Exp 1: within boundary	270°	Aligned, Misaligned	Within	Yes	Yes	Allocentric
Exp 2	270°	Aligned, Misaligned	Across	No	Yes	Allocentric
Exp 3	270°	Aligned, Misaligned	Across	Yes	No	Allocentric
Exp 4: including learning orientation	90°	Aligned, Misaligned, Imagined 90	Across	Yes	Yes	Allocentric
Exp 4: excluding learning orientation	270°	Aligned, Misaligned, Imagined 90	Across	Yes	Yes	Allocentric
Exp 5	90°	Aligned, Misaligned, Imagined 90	Across	Yes	Yes	Egocentric
Exp 6	90°	Aligned, Misaligned, Imagined 90, Imagined 270	Across	Yes	Yes	Allocentric

2.3.1 Method

2.3.1.1 Participants

The study was approved by the Ethics Committee of the University of Alberta. Sixty-four university students (32 females) with normal or corrected-to-normal vision participated to partially fulfill the requirement for an introductory psychology course. Thirty-two participants (16 females) were assigned to each of the two boundary conditions. Hence, sensorimotor alignment is a within-subject variable, whereas boundary condition is a between-subject variable. The power to detect a significant main effect of sensorimotor alignment is 0.78 at the alpha level of .05 using a mixed-design ANOVA, assuming the partial eta squared (η_{p}^2) is 0.11[1] (see the Matlab code for the power analysis at https://doi.org/10.7939/r3-aqm4-3p16).

2.3.1.2 Materials and design

The real experimental lab space had two square rooms (4.4 m by 4.4 m each) and a hallway (Figure 2.1A). Each room had systems of virtual environments and motion tracking. The immersive virtual environment was presented using Vizard software (WorldViz, Santa Barbara, CA) in a head-mounted display (HMD, Oculus Rift, Oculus VR, LLC., Irvine, CA). The participants' head motions were tracked by an InterSense IS-900 motion tracking system (InterSense, Inc., Massachusetts) so that they could physically walk and turn to change their viewpoints in the virtual environment. During learning, when the participants were asked to replace the objects, they used a pointing device (an InterSense Wand) to control a virtual blue stick. In the JRD task, the participants used a joystick (Logitech Extreme 3D Pro, Newark, CA) to judge the relative direction to a target from an imagined perspective.

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[1] η_{p}^2 of 0.11 in a F(1,62) test is comparable to Cohen's *d* of 0.5, a medium effect. $d = \sqrt{\frac{2\times(\mathrm{N}-1)\times\eta 2}{N\times(1-\eta 2)}}$. N is the participant number in each boundary condition.

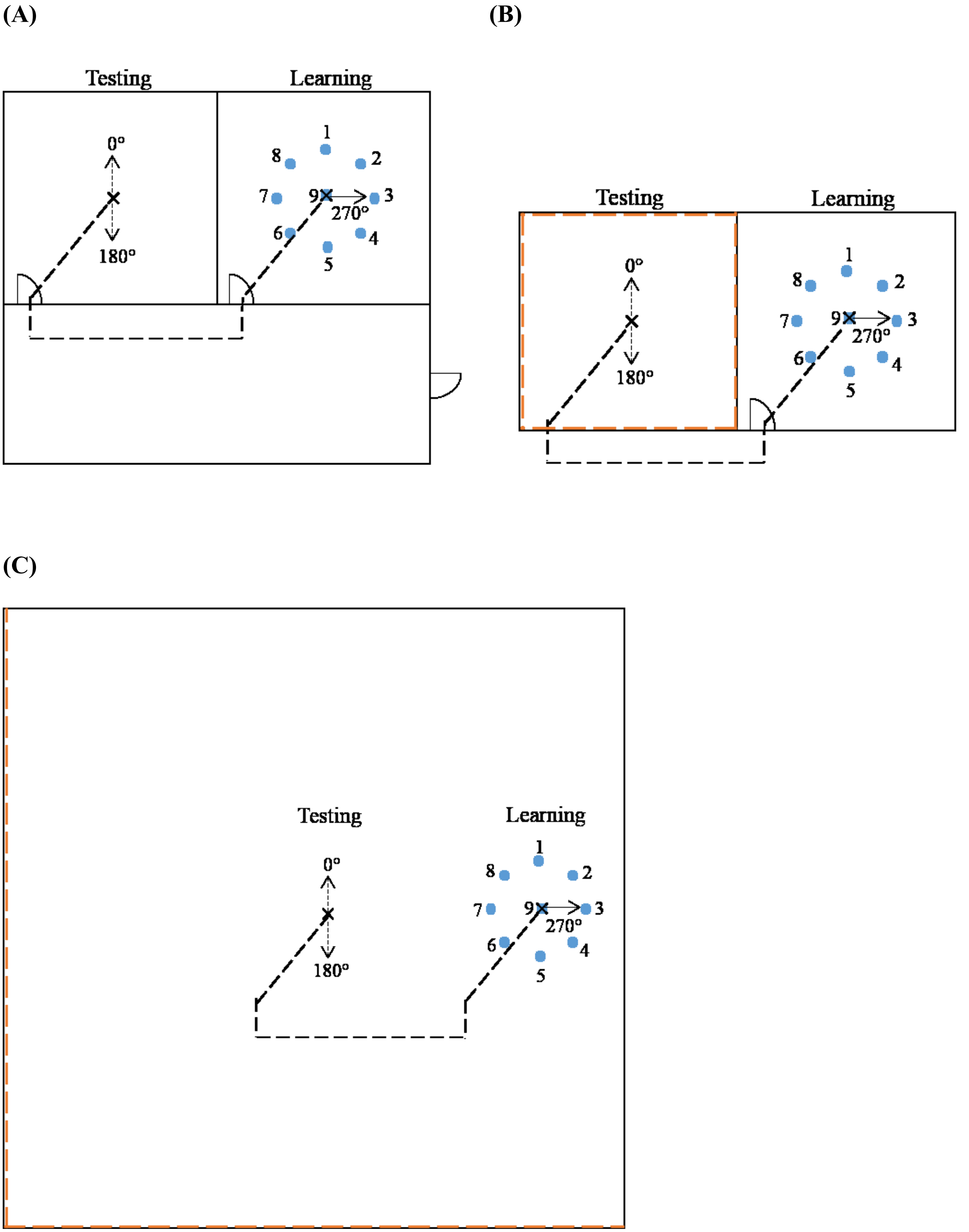

(A)
Testing
Learning
0°
180°
1
2
3
4
5
6
7
8
9
270°
(B)
Testing
Learning
0°
180°
1
2
3
4
5
6
7
8
9
270°
(C)
Testing
Learning
0°
180°
1
2
3
4
5
6
7
8
9
270°

Figure 2. 1 Top view of schematic experimental setup in Experiment 1. (A) Real lab spaces with two physical rooms and a hallway. (B) Two virtual rooms in the across-boundary condition. (C) One virtual room in the within-boundary condition. The dashed red lines along the room walls indicate red walls. The blue dots and the numbers are the objects. The crosses are the learning and testing positions. The solid arrow is the learning orientation (270°). The dashed line is the walking route from the learning position to the testing position. The dashed arrows are the physical perspectives (0°, 180°) in the testing phase.

For all the participants, the learning position, testing position, and walking path were the same in the real lab space. The learning position was the centre of one real lab room, and the testing position was the centre of the other real lab room. The walking path was from the learning position to the testing position. The participants only saw the virtual environments and did not at any point see the real lab space. Nine virtual objects were presented on the ground, with one object in the middle and the other eight objects evenly distributed every 45° in a circle (radius=1.8 m). The learning position was in the middle of this circular array (i.e., object 9 in Figure 2.1). There were also real objects placed on the ground at the locations such that the virtual objects overlapped with the real objects. These real objects were placed for the participants to physically touch to increase the reality of the virtual environments.

The across-boundary and within-boundary conditions (a between-subject variable) had different virtual environments. In the across-boundary condition, the virtual environment consisted of two square rooms (4.4 m by 4.4 m each), with one for learning and the other for testing (Figure 2.1B). They overlapped with the real lab rooms. The learning position was the centre of the virtual learning room, and the testing position was the centre of the virtual testing room. The virtual learning and testing rooms were visually different. The virtual learning room had a door that overlapped with the door in the real lab room, and it had four white walls with hexagon patterns. The virtual testing room did not have a door, and it had four red walls with brick patterns. In the within-boundary condition, the virtual environment presented one square room (13.2 m by 13.2 m) (Figure 2.1C). This virtual room was created with the testing position as the centre of the room and its right wall overlapping the right wall of the real lab room for learning. The virtual room did not have a door, and it had two adjacent walls that were red with brick patterns while the other two walls were white with hexagon patterns. Thus, for across-boundary and within-boundary conditions, the participants' physical learning and testing locations and also the walking path between the locations were the same in the real lab space. The virtual environments made the learning, testing, and walking take place in across-boundary or within-boundary conditions.

Furthermore, the participants in different boundary conditions received different instructions about the ending position of their walking towards the testing position. In the across-boundary condition, the participants were told that they would walk to another position in a different room, whereas in the within-boundary condition, the participants were told that they would walk to another position within the same room. When walking outside the real lab room for learning, the participants in the across-boundary condition were instructed to touch the real door, whereas the participants in the within-boundary condition did not touch anything. In addition, after reaching the testing position, the participants in the across-boundary condition were reassured that they had walked to another position in a novel room, whereas the participants in the within-boundary condition were told that they had walked to another position in the same room.

The second independent variable (i.e., sensorimotor alignment) is specified by the relation between the participants' physical perspective and the imagined perspective in the JRD task. For each JRD trial, the locations specifying the imagined perspectives and the target location were all from the remembered object array (e.g., imagine you are standing at object 4 and facing object 2, point to object 5).

The participants' physical perspectives were 0° and 180° at the physical testing position, and the imagined perspectives were also 0° and 180° inside of the remembered array of objects (Figure 2.1). Depending on the alignment between the physical and imagined perspectives, there were two types of trials: sensorimotor aligned and sensorimotor misaligned (within-subject variable). Table 2.2 shows the physical and imagined perspectives for each trial type (aligned or misaligned in Table 2.2 for Experiment 1).

The JRD task was blocked by the two physical perspectives. In each block, 16 trials were generated for each imagined perspective (0° or 180° in Table 2.3), producing 32 trials. The order of the blocks (i.e., the two physical perspectives) was counterbalanced across the participants, and the order of the trials within each block was randomized for each participant.

Therefore, this experiment used a mixed design, with one between-subject variable (boundary condition: across-boundary, within-boundary) and one within-subject variable (sensorimotor alignment: aligned, misaligned). The dependent variables were the absolute angular error and response latency in the pointing responses of the JRD task.

Table 2. 2 Imagined and physical perspectives in the four trial types used in the current study. Trial types of aligned and misaligned were used in Experiments 1-3. Trial types of aligned, misaligned, and imagined 90 were used in Experiments 4-5. Trial types of aligned, misaligned, imagined 90, and imagined 270 were used in Experiment 6.

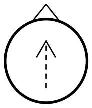
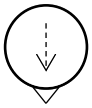
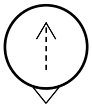
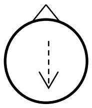
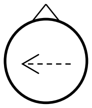
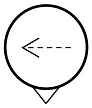
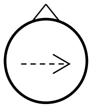
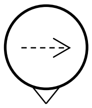
Trial type	Imagined and physical perspectives			
Aligned	Imagined 0 Physical 0		Imagined 180 Physical 180	
Misaligned	Imagined 0 Physical 180		Imagined 180 Physical 0	
Imagined 90	Imagined 90 Physical 0		Imagined 90 Physical 180	
Imagined 270	Imagined 270 Physical 0		Imagined 270 Physical 180	

Table 2. 3 The standing, facing, and target objects for all imagined perspectives used in Experiments 1, 2, 3, 4, and 6 (see Table 2.4 for Experiment 5). Imagined perspectives of 0° and 180° were used in Experiments 1-3. Imagined perspectives of 0°, 90°, and 180° were used in Experiment 4. Imagined perspectives of 0°, 90°, 180°, and 270° were used in Experiment 6.

Imagined perspective	Standing object	Facing object	Target object
0°	9	1	2; 3; 4; 6; 7; 8
	5	9	2; 4; 6; 8
	6	8	1; 5; 7
	4	2	1; 3; 5
90°	9	7	1; 2; 4; 5; 6; 8
	3	9	2; 4; 6; 8
	4	6	3; 5; 7
	2	8	1; 3; 7
180°	9	5	2; 3; 4; 6; 7; 8
	1	9	2; 4; 6; 8
	2	4	1; 3; 5
	8	6	1; 5; 7
270°	9	3	1; 2; 4; 5; 6; 8
	7	9	2; 4; 6; 8
	8	2	1; 3; 7
	6	4	3; 5; 7

2.3.1.3 Procedure

Before the experiment, the participants signed consent forms, read instructions, and practiced how to use a joystick to point. Next, the participants were blindfolded and guided on a circuitous path to the centre of the real lab room for learning (i.e., the learning position, object 9 in Figure 2.1). They faced the learning orientation of 270° (i.e., facing the right wall in Figure 2.1). Then they were required to close their eyes, remove their blindfold and put on the HMD.

In the learning phase, the participants first looked around the room and went to touch the wall in front of them (i.e., the right wall in Figure 2.1). Then they returned to the learning position and the learning orientation, and the objects were presented. The participants named the objects with the help of the experimenter. Then, they were instructed to touch three objects (the object at 3 that was in front of them, the object at 6 that was on the walking path, and another random object). To touch each object, they started from the learning position, went to touch the object, and then returned to the learning position. Touching the wall and the objects helped the participants calibrate their movement in the virtual environment with the real lab space and also made the participants feel the virtual environment was as stable as the real environment (Mohler, Creem-Regehr, & Thompson, 2006; Siegel, Kelly, & Cherep, 2017; Taube, Valerio, & Yoder, 2013). Next, the participants returned to the learning orientation and were given three minutes to learn the objects' locations while standing at the learning position and facing the learning orientation. After three minutes, the objects disappeared, and the participants replaced the objects. To replace an object, the probed object with its name appeared at the centre of the HMD, and the participants controlled the virtual stick to replace it. The object was shown at the replaced location and also at the correct location as feedback. The replaced locations were recorded. There were three blocks to replace the objects, and the order of the objects was randomized in each block. After this, the objects were presented until the participants reported that they had good memories of the objects' locations. The learning phase ended.

Between the learning and testing phases, several extra steps were used to increase the likelihood that the participants updated their self-location in the virtual environments just as in the real environments. After learning and while still taking the learning viewpoint (i.e., standing at object 9 and facing object 3 as in Figure 2.1), the participants closed their eyes, took off the HMD, and put on the blindfold. They were instructed to use their fingers to point to some objects that were randomly named by the experimenter. Then, they were asked to turn to face object 6 (Figure 2.1), and they pointed to the randomly named objects as requested. After completing this, they removed the blindfold and put on the HMD to see the virtual environment from a new viewpoint (i.e., standing at object 9 and facing object 6 as in Figure 2.1). To further motivate the participants to update their viewpoints, they were asked to replace all the objects once without feedback. The replaced locations were recorded. After replacing the objects, they closed their eyes to take off the HMD and put on the blindfold. Next, they were guided to walk from object 9 to object 6 (Figure 2.1). Again, at the new location (object 6), they first used their fingers to point to objects named by the experimenter and then put on the HMD to replace all the objects once without feedback. After replacing the objects, they closed their eyes to take off the HMD and put on the blindfold. All these means were used to make the participants understand that the objects were stabilized relative to the environment rather than stabilized relative to their bodies during locomotion (Mou, Li, & McNamara, 2008).

Then, the participants were instructed about the ending position of their walking, either being a different position in the same room or a different position in a novel room. When walking outside the real lab room for learning, the participants in the across-boundary condition touched the real door. The participants in both conditions were instructed to pay attention to their walking and keep track of the objects during walking. The blindfolded participants were led to walk a path (i.e., represented by the dashed lines in Figure 2.1) to the testing position and then were oriented to face a physical perspective (i.e., 0° or 180°, represented by the dashed arrows in

Figure 2.1). Then, they closed their eyes, removed the blindfold, and put on the HMD in the real testing room. The participants were then told that they had walked to another position in a novel room or another position in the same room.

The testing phase started. In the testing phase, the participants stood at the testing position and were given a joystick to conduct the JRD task. For each physical perspective (i.e., 0° or 180°), they finished one block of the JRD trials. In each trial, one sentence to instruct an imagined perspective was presented at the centre of the HMD screen (e.g., “standing at the lock, facing the candle”). The participants were required to keep their physical perspective and mentally take the imagined perspective. They clicked the trigger on the joystick if they took the imagined perspective. The duration between the presentation of the imagined perspective and the clicked trigger was recorded as orientation latency. After the participants clicked the trigger, the first sentence disappeared, and another sentence was presented to instruct a target object (e.g., “point to the mug”). The participants were required to keep their physical perspective and use the joystick to point to the target from the imagined perspective. They were asked to respond as fast as possible without sacrificing accuracy. The duration between the presentation of the target and the response was recorded as response latency. The response direction was also recorded to calculate the absolute angular pointing error. After the participants responded, the second sentence disappeared. The next trial started after 750 ms.

2.3.2 Results

We calculated the mean orientation latency, mean response latency, and mean absolute angular pointing error in each trial type. We conducted ANOVAs for all these measures with one between-subject factor (boundary condition: across-boundary, within-boundary) and one within-subject factor (sensorimotor alignment: aligned, misaligned).

There were no significant effects for orientation latency in all experiments of the current study (Figure S2.1 in the supplementary materials). Thus, for this and the following experiments, we only report detailed results from response latency and absolute pointing error.

2.3.2.1 Response latency

Figure 2.2 shows the mean response latency for each sensorimotor alignment and each boundary condition. The main effect of boundary was not significant, $F(1, 62) = 1.77, p = .189$, $\eta_p^2 = 0.03$. The main effect of sensorimotor alignment was significant, $F(1, 62) = 12.09, p = .001$, $\eta_p^2 = 0.16$ (comparable to Cohen's $d = 0.62$), showing that the responses in the aligned trials were faster than those in the misaligned trials. The interaction between boundary and sensorimotor alignment was not significant, $F(1, 62) = 0.00, p = .995$, $\eta_p^2 = 0.00$, showing that the sensorimotor alignment effect was not different in across-boundary and within-boundary conditions. A Bayes factor analysis favouring the null effect over the alternative[2] supported the null interaction effect, $BF_{01}=5.30$.

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[2] The null effect is favoured if the BF_{01} is larger than three and strongly favoured if the BF_{01} is larger than 10. The alternative effect is favoured if the BF_{01} is smaller than 1/3 and strongly favoured if the BF_{01} is smaller than 1/10 (Rouder, Speckman, Sun, Morey, & Iverson, 2009). If the BF_{01} is between 1/3 and three, neither is favoured.

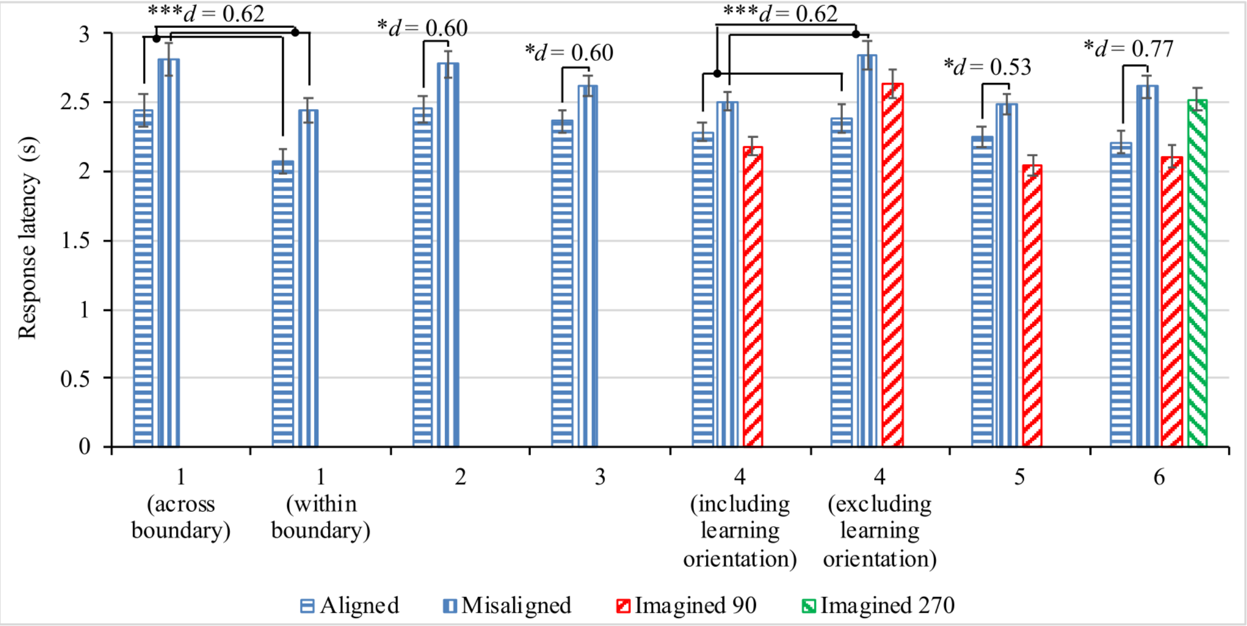

Figure 2. 2 The mean response latency for each trial type in all experiments. Error bars represent ±1 SE removing the variance from individual differences. The solid line means a significant sensorimotor alignment effect (the comparison between aligned and misaligned conditions) (p< .05; ** p< .01; *** p< .001). Values for Cohen's d are listed.*

2.3.2.2 Absolute pointing error

Figure 2.3 shows the mean absolute angular pointing error as a function of sensorimotor alignment and boundary condition. The main effect of boundary was not significant, $F(1, 62) = 0.89$, $p = .349$, $\eta_p^2 = 0.01$. The main effect of alignment was significant, $F(1, 62) = 7.20$, $p = .009$, $\eta_p^2 = 0.10$ (comparable to Cohen's $d = 0.48$), showing more accurate responses in the aligned trials than in the misaligned trials. The interaction between boundary and sensorimotor alignment was not significant, $F(1, 62) = 0.80$, $p = .374$, $\eta_p^2 = 0.01$, showing that the sensorimotor alignment effect was not different in across-boundary and within-boundary conditions. A Bayes factor analysis (BF_{01}= 3.67) supported the null interaction effect.

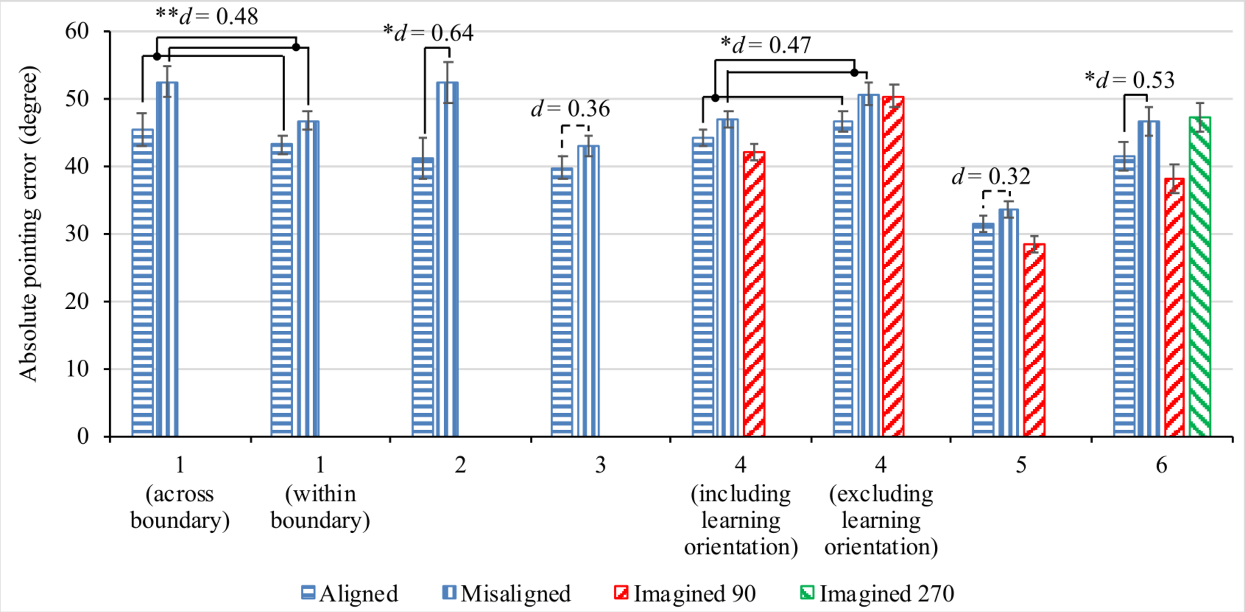

Figure 2. 3 The mean absolute pointing error for each trial type in all experiments. Error bars represent ±1 SE removing the variance from individual differences. The solid line means a significant sensorimotor alignment effect (the comparison between aligned and misaligned conditions), and the dashed line means an insignificant effect (p< .05; ** p< .01; *** p< .001). Values for Cohen's d are listed.*

2.3.3 Discussion

The results in Experiment 1 showed comparable sensorimotor alignment effects in within-boundary and across-boundary conditions, demonstrating that the participants updated their global headings by one-shot walking equally well when walking across boundaries and walking within the same boundary. These results support that people can update headings relative to a global environment and develop global spatial representations by one-shot walking. In addition, boundaries do not impair updating in the global environment. The following experiments (2-6) were only centred on one-shot across-boundary walking and further examined factors that could affect updating global headings and developing global representations.

Experiments 2-3 tested two factors that might affect the global updating of self-location. Specifically, the first factor was the instruction for attention and tracking the objects in across-boundary walking, which might have explicitly required the participants to relate their self-location on the walking path with the objects in the learning room. The second factor was the existence of the door in the virtual learning room, which might have served as a visual cue to provide navigational affordance linking to another space and might have helped the development of global memories across boundaries.

2.4 Experiment 2

In Experiment 1, the participants were instructed to pay attention to walking and keep track of the objects during walking. Experiment 2 tested whether the instruction to attend to walking and track the objects was essential to update headings relative to a global environment. Previous studies have shown that spatial updating of headings relative to immediate spaces appears to be automatic (Farrell & Robertson, 1998; Rieser, 1989). However, Wang (2004) showed that updating relative to a remote space (an imagined space) seems to not be automatic. The current Experiment 2 removed these instructions for attention to the updating process. If the results still showed a sensorimotor alignment effect, then global updating and developing global representations by one-shot across-boundary walking is automatic, in the sense that it does not require explicit instructions for attention, whereas if the results showed no sensorimotor alignment effect, then attention to the updating process is needed to update global headings after one-shot walking across boundaries.

2.4.1 Method

2.4.1.1 Participants

Thirty-two university students (16 females) with normal or corrected-to-normal vision participated to partially fulfill the requirement for an introductory psychology course. The power was 0.66 at the alpha level of .05 for 32 participants to detect $\eta_p^2 = 0.16$, which was the observed effect size for the sensorimotor alignment effect in Experiment 1.

2.4.1.2 Materials, design, and procedure

The materials, design, and procedure were the same in Experiment 2 as for the across-boundary condition in Experiment 1 except that, prior to walking, the participants did not receive the instruction to pay attention to walking and keep track of the objects during walking.

2.4.2 Results

2.4.2.1 Response latency

Figure 2.2 plots the mean response latency for each sensorimotor alignment. The responses in the aligned trials were significantly faster than those in the misaligned trials, $t(31) = 2.41$, $p = .022$, Cohen's $d = 0.60$ (comparable to $\eta_p^2 = 0.15$), demonstrating a sensorimotor alignment effect.

2.4.2.2 Absolute pointing error

Figure 2.3 shows the results in the mean absolute angular pointing error. The responses in the aligned trials were significantly more accurate than those in the misaligned trials, $t(31) = 2.58$, $p = .015$, Cohen's $d = 0.64$ (comparable to $\eta_p^2 = 0.17$), demonstrating a sensorimotor alignment effect.

2.4.3 Discussion

The results in Experiment 2 showed a sensorimotor alignment effect, suggesting that updating and developing global representations by one-shot across-boundary walking is automatic in the sense that it does not require explicit instruction for attention to the updating process.

2.5 Experiment 3

Experiment 3 tested whether a visual cue indicating navigational affordance to other spaces is important to updating headings relative to global relations and developing global memories after one-shot across-boundary walking. Specifically, it tested whether the door of the learning room is important for updating headings relative to global relations. Previous studies have shown that, in scene perception, people automatically identify navigational affordance in a scene, which is the identification of where one can move to, such as to a door or an unobstructed path (Bonner & Epstein, 2017; Greene & Oliva, 2009). In Experiments 1-2, the door of the learning room might have provided navigational affordance to another space. This might have helped to support updating relative to global relations and developing global memories. When participants walked through virtual walls instead of doors, the global updating process might have been impaired (Kelly et al., 2007). Experiment 3 removed the door in the virtual learning room. If the results still showed a sensorimotor alignment effect, then the visual cues for navigational affordance between spaces are not important to global updating and developing global memories based on one-shot across-boundary walking.

2.5.1 Method

2.5.1.1 Participants

Thirty-two university students (16 females) with normal or corrected-to-normal vision participated to partially fulfill the requirement for an introductory psychology course.

2.5.1.2 Materials, design, and procedure

The materials, design, and procedure were the same in Experiment 3 as for the across-boundary condition in Experiment 1, except that there was no door in the virtual learning room, and the participants did not touch the door of the real lab room when walking outside the learning room.

2.5.2 Results

2.5.2.1 Response latency

Figure 2.2 shows the results of the mean response latency. The responses in the aligned trials were significantly faster than those in the misaligned trials, $t(31) = 2.38$, $p = .024$, Cohen's $d = 0.60$, demonstrating a sensorimotor alignment effect.

2.5.2.2 Absolute pointing error

Figure 2.3 shows the results of the mean absolute angular pointing error. The responses in the aligned trials were not significantly different from those in the misaligned trials, $t(31) = 1.44$, $p = .161$, Cohen's $d = 0.36$, although the trend was consistent with a sensorimotor alignment effect.

2.5.3 Discussion

The results in Experiment 3 showed a sensorimotor alignment effect, suggesting that visual cues indicating navigational affordance between spaces are not necessary to update headings relative to global relations and develop global representations by one-shot across-boundary walking.

Experiments 1-3 consistently showed sensorimotor alignment effects after one-shot across-boundary walking, indicating that the participants developed global representations by one-shot walking and also relied on the global representations in the JRD task. In contrast, in Kelly et al. (2007), the participants did not show sensorimotor alignment effects after one-shot walking into a visually and spatially different room. The participants in their study might also have developed global memories. However, some properties of the JRD task might have made the participants in their study only rely on the original self-localization representations in long-term memory (i.e., encoding their original learning viewpoint relative to the object array) instead of the global representations developed by walking. Experiments 4-6 examined three factors of JRD trials that might modulate the use of updated global representations or the original representations in long-term memory. Specifically, Experiment 4 examined the first factor of including the learning orientation as one of the imagined perspectives, as including the learning orientation might activate the original representations in long-term memory. The second factor was to let the participants imagine themselves standing at the learning position and then conduct egocentric pointing to make the testing scenario more similar to the learning scenario. The third factor was to increase the task difficulty by testing more imagined perspectives. The original representations in long-term memory were well developed during learning compared with the global representations developed by walking. When the number of imagined perspectives increased, taking imagined perspectives might be easier by using the original representations in long-term memory rather than using global representations.

2.6 Experiment 4

Experiment 4 tested whether including the learning orientation as one of the imagined perspectives in the JRD task would affect the use of the global representations developed by one-shot across-boundary walking. Since the learning orientation was encoded in the originally formed spatial representations in long-term memory, including the learning orientation as an imagined perspective might encourage the use of the original representations and discourage the use of the global representations. All previous experiments in the current study excluded the learning orientation from the imagined perspectives in the JRD trials (see Table 2.1), and this exclusion might have led to clear sensorimotor alignment effects.

In Experiment 4, after across-boundary walking, the participants conducted the task with the imagined perspectives either including the learning orientation or excluding the learning orientation. If including the learning orientation as an imagined perspective does not influence the use of global representations, then there would be sensorimotor alignment effects whether the imagined perspectives included or excluded the learning orientation. By contrast, if including the learning orientation as an imagined perspective impairs the use of global representations, then there would be a sensorimotor alignment effect only when the imagined perspectives excluded the learning orientation.

2.6.1 Method

2.6.1.1 Participants

Sixty-four university students (32 females) with normal or corrected-to-normal vision participated to partially fulfill the requirement for an introductory psychology course. Thirty-two of them (16 females) were assigned to each of the conditions of including or excluding the learning orientation.

2.6.1.2 Materials, design, and procedure

The materials, design, and procedure were the same in Experiment 4 as for the across-boundary condition in Experiment 1 except for the following differences. First, the learning orientation was manipulated to be either 90° or 270° for the conditions of the learning orientation as included or excluded in the imagined perspectives. Second, the imagined perspectives were 0°, 90°, and 180°. Thus, in addition to the two types of trials used in Experiments 1 and 2 (i.e., aligned and misaligned), there was an additional type of trial: imagined 90 (Table 2.2). As a result, the group of participants who learned at 90° would have imagined perspectives including the learning orientation, while those who learned at 270° would have imagined perspectives excluding the learning orientation. For imagined 90, there were also 16 trials (Table 2.3), producing 48 trials in total for each of the two blocks.

Therefore, this experiment used a mixed design, with one between-subject variable (learning orientation: included, excluded) and one within-subject variable (trial type: aligned, misaligned, imagined 90).

2.6.2 Results

We conducted ANOVAs with one between-subject factor (learning orientation: included, excluded) and one within-subject factor (trial type: aligned, misaligned, imagined 90) on mean orientation latency, mean response latency, and mean absolute angular pointing error.

2.6.2.1 Response latency

Figure 2.2 shows the mean response latency for each learning orientation condition and for each trial type. The main effect of learning orientation was not significant, $F(1, 62) = 1.81$, $p = .184$, $\eta_p^2 = 0.03$. The main effect of trial type was significant, $F(2, 124) = 7.74$, $p = .001$, $\eta_p^2 = 0.11$. The interaction between learning orientation and trial type was not significant, $F(2, 124) = 2.10$, $p = .127$, $\eta_p^2 = 0.03$. Pairwise comparisons showed that the aligned trials were significantly faster than the misaligned trials, $t(63) = 3.49$, $p = .001$, Cohen's $d = 0.62$; the imagined 90 trials were also significantly faster than the misaligned trials, $t(63) = 2.71$, $p = .009$, Cohen's $d = 0.48$; however, the aligned trials were not different from the imagined 90 trials, $t(63) = 0.99$, $p = .326$, Cohen's $d = 0.17$. These results showed sensorimotor alignment effects for both groups of the participants whether the learning orientation was included or excluded in the imagined perspectives.

2.6.2.2 Absolute pointing error

Figure 2.3 shows the mean pointing error for each learning orientation condition and for each trial type. The main effect of learning orientation was not significant, $F(1, 62) = 1.08$, $p = .302$, $\eta_p^2 = 0.02$. The main effect of trial type was not significant, $F(2, 124) = 3.05$, $p = .051$, $\eta_p^2 = 0.05$. The interaction between learning orientation and trial type was not significant, $F(2, 124) = 2.31$, $p = .103$, $\eta_p^2 = 0.04$. Pairwise comparisons showed that the aligned trials were significantly faster than the misaligned trials, $t(63) = 2.63$, $p = .011$, Cohen's $d = 0.47$; however, the other two comparisons were not significant (imagined 90 versus misaligned trials: $t(63) = 1.84$, $p = .070$, Cohen's $d = 0.33$; aligned versus imagined 90 trials, $t(63) = 0.51$, $p = .609$, Cohen's $d = 0.09$). These results showed sensorimotor alignment effects for both groups of the participants whether the learning orientation was included or excluded as an imagined perspective.

2.6.3 Discussion

The results in Experiment 4 showed sensorimotor alignment effects in both conditions when the imagined perspectives included and excluded the learning orientation. This suggests that whether or not the learning orientation was included as one of the imagined perspectives does not influence the use of the global representations developed by one-shot walking across boundaries.

2.7 Experiment 5

In Experiments 1-4, participants performed allocentric pointing in which their imagined standing positions were varied for each imagined perspective (see Table 2.3). Although Experiment 4 included the learning orientation in the imagined perspectives, the imagined positions were different from the original learning position (i.e., object 9 in Figure 2.1) in the majority of trials (10 out of 16 trials for imagined perspective 90° in Table 2.3). One may argue that the original spatial representations formed in the learning phase are more likely to be used instead of the updated global representations in the JRD task when both the imagined position and orientation are the same as the learning position and orientation. Kelly et al. (2007) asked the participants to perform egocentric pointing by always imagining standing at the learning position and taking different imagined perspectives (e.g., "imagine facing A," "point to B"). The egocentric pointing from the learning position, which was more similar to the learning scenario, might encourage the participants to use the original spatial representations in long-term memory developed from the learning viewpoint. This might have suppressed the use of the global representations that had been developed by one-shot across-boundary walking.

Experiment 5 asked the participants to perform egocentric pointing by always imagining standing at the learning position and taking different imagined perspectives (e.g., "imagine facing the mug," "point to the wood"). If the participants did not show a sensorimotor alignment effect, then the egocentric pointing would discourage the use of global representations after one-shot across-boundary walking.

2.7.1 Method

2.7.1.1 Participants

Thirty-two university students (16 females) with normal or corrected-to-normal vision participated to partially fulfill the requirement for an introductory psychology course.

2.7.1.2 Materials, design, and procedure

The materials, design, and procedure were the same in Experiment 5 as for the group that included the learning orientation in Experiment 4 except for the following differences. First, the participants were instructed to imagine standing at the learning position (i.e., object 9 in Figure

2.1) in the learning room to conduct the JRD task. Accordingly, for each trial, the sentence that instructed an imagined perspective only mentioned the facing object but not the standing object (e.g., “imagine facing the mug”). Second, for each of the three imagined perspectives (i.e., 0°, 90°, and 180°, which correspond to standing at 9 and imagining facing 1/7/5 in Figure 2.1), seven trials were generated using all of the other seven objects as targets (e.g., if imagining facing 1, then all possible targets were 2-8) (see Table 2.4). To increase power, there were two blocks of these trials for each of the two physical perspectives. The trials were randomized in each block. Thus, there were 42 trials for each physical perspective (14 for each trial type, i.e., aligned, misaligned, or imagined 90).

Table 2. 4 The standing, facing, and target objects for all imagined perspectives used in Experiment 5.

Imagined perspective	Standing object	Facing object	Target object
0°	9	1	2; 3; 4; 5; 6; 7; 8
90°	9	7	1; 2; 3; 4; 5; 6; 8
180°	9	5	1; 2; 3; 4; 6; 7; 8

2.7.2 Results

We conducted ANOVAs with one within-subject factor (trial type: aligned, misaligned, imagined 90).

2.7.2.1 Response latency

Figure 2.2 shows the mean response latency for each trial type. The main effect of trial type was significant, $F(2, 62) = 9.01$, $p < .001$, $\eta_p^2 = 0.23$. Pairwise comparisons showed that the aligned trials were significantly faster than the misaligned trials, $t(31) = 2.12$, $p = .042$, Cohen’s *d* = 0.53; the imagined 90 trials were also significantly faster than the misaligned trials, $t(31) = 4.37$, $p < .001$, Cohen's $d = 1.09$; however, the aligned trials were significantly slower than the imagined 90 trials, $t(31) = 2.07$, $p = .047$, Cohen's $d = 0.52$. These results showed a sensorimotor alignment effect in addition to the effect from the benefit of the learning orientation (i.e., 90°).

2.7.2.2 Absolute pointing error

Figure 2.3 plots the mean absolute angular pointing error. The main effect of trial type was significant, $F(2, 62) = 4.56$, $p = .014$, $\eta_p^2 = 0.13$. Pairwise comparisons showed the only significant comparison was that the imagined 90 trials were significantly more accurate than the misaligned trials, $t(31) = 3.27$, $p = .003$, Cohen's $d = 0.82$. The aligned trials were not significantly different from the misaligned trials ($t(31) = 1.27$, $p = .215$, Cohen's $d = 0.32$) or the imagined 90 trials ($t(31) = 1.61$, $p = .118$, Cohen's $d = 0.40$).

2.7.3 Discussion

The results in Experiment 5 showed a sensorimotor alignment effect from a JRD task only using egocentric pointing. This suggests that the use of the global representations developed by one-shot across-boundary walking does not rely on the task requirement for egocentric pointing or not.

2.8 Experiment 6

Experiment 6 tested whether more imagined perspectives would affect the use of global representations developed by one-shot across-boundary walking. The representations of objects' locations encoded at the learning viewpoint in long-term memory should be well-developed and enduring since the participants extensively learned the objects at the learning viewpoint. By contrast, the global representations developed by one-shot across-boundary walking might be coarser and transient. It is possible that people would prefer well-developed and enduring spatial representations over coarser and transient spatial representations when the JRD task becomes more complex (e.g., with increased and more varied perspectives). In Experiment 6, the participants were tested with four imagined perspectives, which was a higher number of imagined perspectives compared with two in Experiments 1-3 and three in Experiments 4-5. If the participants still showed a sensorimotor alignment effect, then this result would suggest that the increased complexity of the imagined perspectives in testing does not affect the use of the global representations.

2.8.1 Method

2.8.1.1 Participants

Thirty-two university students (16 females) with normal or corrected-to-normal vision participated to partially fulfill the requirement for an introductory psychology course.

2.8.1.2 Materials, design, and procedure

The materials, design, and procedure were the same in Experiment 6 as for the group that included the learning orientation in Experiment 4 except that the imagined perspective of 270° was added to the JRD task (see the trial type of imagined 270 in Table 2.2 and trial information in Table 2.3) and thus there were 64 trials for each of the two blocks in the JRD task.

2.8.2 Results

We conducted ANOVAs with one within-subject factor (trial type: aligned, misaligned, imagined 90, imagined 270).

2.8.2.1 Response latency

Figure 2.2 plots the mean response latency for each trial type. The main effect of trial type was significant, $F(3, 93) = 8.72$, $p < .001$, $\eta_p^2 = 0.22$. Pairwise comparisons showed that the aligned trials were significantly faster than both the misaligned trials and the imagined 270 trials

($t(31) = 3.07$, $p = .004$, Cohen's $d = 0.77$; $t(31) = 2.69$, $p = .011$, Cohen's $d = 0.67$, respectively), but the aligned trials were not different from the imagined 90 trials ($t(31) = 1.17$, $p = .252$, Cohen's $d = 0.29$). The imagined 90 trials were significantly faster than both the misaligned trials and the imagined 270 trials ($t(31) = 5.04$, $p < .001$, Cohen's $d = 1.26$; $t(31) = 3.20$, $p = .003$, Cohen's $d = 0.80$, respectively). The misaligned trials and the imagined 270 trials were not different from each other ($t(31) = 0.74$, $p = .465$, Cohen's $d = 0.18$). These results showed a sensorimotor alignment effect in addition to the learning orientation effect.

2.8.2.2 Absolute pointing error

Figure 2.3 shows the mean absolute angular pointing error. The main effect of trial type was significant, $F(3, 93) = 4.17$, $p = .008$, $\eta_p^2 = 0.12$. Pairwise comparisons showed that the participants were significantly more accurate in the aligned trials than in the misaligned trials and the imagined 270 trials ($t(31) = 2.12$, $p = .042$, Cohen's $d = 0.53$; $t(31) = 2.28$, $p = .030$, Cohen's $d = 0.57$, respectively), but the aligned trials were not different from the imagined 90 trials ($t(31) = 1.40$, $p = .172$, Cohen's $d = 0.35$). The responses in the imagined 90 trials were significantly more accurate than those in the misaligned trials and the imagined 270 trials ($t(31) = 3.03$, $p = .005$, Cohen's $d = 0.76$; $t(31) = 2.18$, $p = .037$, Cohen's $d = 0.54$, respectively). The misaligned trials and the imagined 270 trials were not different from each other ($t(31) = 0.21$, $p = .835$, Cohen's $d = 0.05$). These results showed a sensorimotor alignment effect in addition to the learning orientation effect.

2.8.3 Discussion

The results in Experiment 6 showed a sensorimotor alignment effect, suggesting that the increased variability of the imagined perspectives in testing does not affect the use of the global representations developed by one-shot across-boundary walking.

2.9 General Discussion

The current study examined developing spatial representations of a global environment by one-shot across-boundary walking. The most important finding was that global sensorimotor alignment effects occurred after one-shot across-boundary walking. Furthermore, this global sensorimotor alignment effect was comparable with the sensorimotor alignment effect after one-shot walking within the same room. In addition, this global sensorimotor alignment effect occurred regardless of instructions for attention and tracking the objects in the learning room, visual cues of the door to another room, including the learning orientation in the testing trials, egocentric pointing in the task, and the number of the imagined perspectives in the task.

The current study for the first time demonstrates that people can update self-location relative to a global environment including two separate rooms and develop global representations by one-shot across-boundary walking. In addition, encoding global relations during novel across-boundary walking seems automatic since it does not require explicit instructions to keep track of the original environment or visual navigational affordance to another room (i.e., the door). The use of global representations developed by novel across-boundary walking may also be automatic since the variables to encourage the use of the original self-localization representations that are formed during learning and stored in long-term memory do not impair the use of global representations to mentally adopt perspectives in the original environment. These results implicate that it may be obligatory to develop global memories and update self-location using global relations by one-shot across-boundary walking.

The demonstration that people can develop global representations after one-shot across-boundary walking provides insight into the relationship between spatial memory and navigation. To conceptualize how people develop spatial memory in a large-scale environment in which people may not directly see spatial relations between two local spaces, some researchers have proposed that people rely on path integration to develop global spatial memory (Gallistel, 1990; Gallistel & Matzel, 2013; Jacobs & Schenk, 2003; Lei et al., 2020; Loomis et al., 1999; McNaughton et al., 2006; Meilinger, 2008). However, other researchers have argued that global spatial memory may not be developed by path integration as path integration is error-prone and may only focus on the immediate space (e.g., Wang, 2016; Warren et al., 2017). Thus, the current study provides clear evidence supporting that people rely on path integration to develop global spatial memory. Note that the current study only demonstrates that people can rely on path integration to develop global spatial memory of two adjacent rooms after walking a relatively simple path. It is still not clear to what extent people can develop global spatial memory after walking a complex path. It is also not clear whether developing global spatial memory after walking a complex path requires extensive navigation experiences and reciprocal interaction between navigation and spatial memory. Future studies are required to understand the role of path complexity and navigation experiences in developing global spatial memory through navigation in a more complex environment.

Previous studies have shown difficulty in developing global representations of multiscale spaces, even after extensive navigational experiences. People may only develop local representations for individual spaces without encoding global relations, and they may shift between local representations when navigating across spaces without relying on global relations (Brokemole & Wang, 2002; Marchette et al., 2014). Developing global representations requires some prerequisites, for example, some prior learning of the global environment or explicit instructions to encode global relations (Han & Becker, 2014; Lei et al., 2020; Shine et al., 2016). We speculate that the inconsistency between the current and previous findings may be reconciled by the complexity of large-scale environments and also by the availability of idiothetic cues during navigation.

First, the number of individual spaces may influence the complexity of large-scale environments. In the current study, the environment only had two rooms with a simple walking path between the rooms. Some previous studies may have used more complex large-scale environments with more individual spaces and more paths between the spaces, for example, a university campus (Brokemole & Wang, 2002) or a large park with four museums (Marchette et al., 2014). The increased number of individual spaces and the increased complexity of the paths linking individual spaces may impair updating self-location relative to global relations and developing global memories, due to the limited capacity in working memory to track spatial relations to multiple spaces (Cowan, 2010) and also the errors accumulated in path integration (Etienne & Jeffery, 2004).

Second, local spaces that are visually similar but globally misaligned may also interfere with developing global representations between local spaces. People can form schematic representations for geometrically equivalent local spaces (Lei et al., 2020; Marchette et al., 2017; Marchette et al., 2014). When local reference directions of two spaces (e.g., the major axis of a rectangular room) are globally misaligned, people may be more likely to rely on local representations (e.g., visual-based re-anchoring, according to Riecke and McNamara, 2017) rather than global representations to update self-location. In the current study, because the learning and testing rooms were both square rooms, there were no conflicting local reference directions in different rooms. The participants could only rely on global representations for self-localization. Future studies may be needed to test whether people can still update self-location relative to the global environment by one-shot walking across spaces when the two spaces are locally similar but globally misaligned.

Third, the participants in the current study physically walked across boundaries, which means they had idiothetic information for both translation and rotation in navigation. However, the participants in some previous studies only navigated with visual cues, such as by using a keyboard to navigate in a desktop virtual environment (e.g., Marchette et al., 2014), or with rotational idiothetic cues, such as by physically rotating but using a joystick to visually translate in a virtual environment (e.g., Lei et al., 2020). Previous studies on the contributions of locomotion modes have shown that idiothetic information during navigation is important to path integration and spatial knowledge acquisition (Chance, Gaunet, Beall, & Loomis, 1998; Chrastil & Warren, 2013; Klatzky et al., 1998; Rieser, 1989; Waller, Loomis, & Haun, 2004). For a large-scale environment, translational idiothetic information may be more important than rotational idiothetic information to encode accurate directions and distances in cognitive maps (Ruddle, Volkova, & Bülthoff, 2011). Thus, the availability of idiothetic information for translation and rotation during navigation may affect the function of path integration to update and develop global memories by one-shot across-boundary navigation.

The experiments in the current study consistently showed sensorimotor alignment effects after the participants physically walked from the learning room to the neighbouring testing room. In contrast, Kelly et al. (2007) showed mixed results. Although they also had the participants physically walk from the learning room to a novel testing room, the results did not show sensorimotor alignment effects unless the testing room looked similar to the learning room. We speculated that the participants in all experiments of Kelly et al. (2007) might also have developed global spatial relations between the learning and testing rooms. This speculation was consistent with the facts that the participants in their study could point to the learning room from the testing room and also could know that they walked back to the original room after walking from the testing room to the learning room. The mixed results of sensorimotor alignment effects might have been due to using the original self-localization representations (encoded from learning viewpoints) stored in long-term memory instead of using the updated self-localization representations in the global environment. The participants could finish a JRD trial using either representation. As speculated in the introduction of this chapter, when the participants walked to the testing room that was visually similar to the learning room, they might have re-anchored themselves back to the learning room, adopting the re-anchored perspective with the location as the learning location (Riecke & McNamara, 2017) but with the same orientation as their walking direction. The participants then turned to the actual headings for testing. They updated their headings from the re-anchored perspective in their representations of the learning room. As the participants' walking direction was coincidentally consistent with the global relations between these two rooms, their updated headings after re-anchoring appeared to be globally correct. By contrast, the participants who saw a visually different testing room might have only retrieved the original self-localization representation after they reached their actual headings in the testing room. Therefore, their different actual headings always appeared to be consistent with their original learning orientation.

The participants in the current study might have used the updated self-localization representations instead of the original self-localization representations. We speculate that the participants in the current study more likely treated the objects in the virtual environments similarly to how they treated the objects in the real environments. In particular, the objects in the environment should be stabilized relative to the environment rather than relative to the participants' bodies when the participants move in the environment (Mou et al., 2004; Mou et al., 2008). Mou et al. (2004) showed that the participants in the virtual environment could be instructed to believe that the objects in the virtual environment could be body-stabilized so that the participants did not update their self-location relative to the objects during locomotion. In the current study, to enable the participants to treat the objects in a manner that was more environment-stabilized, we let the participants move to touch the real wall and also several real objects in the learning room. In addition, the virtual environments and the locomotion mode (i.e., physical walking) were more naturalistic in the current study. In contrast, the participants in Kelly et al. (2007) only visually viewed the objects' locations from the learning orientation. The participants also visually saw themselves walking through a virtual wall into another room. Therefore, they might have been less likely to perceive the similarity of virtual and real environments and thus might have been more likely to use body-stabilized updating during locomotion.

In addition, the statistical power of using 16 participants in each experiment of Kelly et al. (2007) might be enough to detect a large effect but not a medium effect. According to the current study, Cohen's *d* of the global sensorimotor alignment effect was about 0.6, indicating a medium effect. In Kelly et al., for the experiments which showed no significant sensorimotor alignment effects, the effect sizes from response latency occasionally appeared to be medium (the partial eta squared value in Experiment 4 was .09). Moreover, the effect sizes from response error could be consistently medium-sized (with partial eta squared being .12 in Experiment 1, .08 in Experiment 2, and .19 in Experiment 4). Thus, after the participants walked to a visually and spatially novel testing room in Kelly et al., there might have been sensorimotor alignment effects which were not detected due to statistical power.

Note that all the above speculations should not be used to undermine the important discovery that visual or spatial similarity between the learning and testing rooms could elicit sensorimotor alignment effects in Kelly et al. (2007), indicating that self-localization representations can be enduring rather than transient. We speculate that the sensorimotor alignment effects in Kelly et al. reflected self-location in a local space, and the sensorimotor alignment effects reported in the current study reflected self-location in a global space.

In conclusion, the current study showed sensorimotor alignment effects after the participants physically walked once across boundaries in a novel environment, indicating that people can update self-location relative to global relations and develop global memories by one-shot walking across boundaries in a novel environment. Boundaries do not affect updating and developing global memories by one-shot walking. In addition, encoding and using global representations may also be automatic.

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2.11 Supplementary materials

2.11.1 Results from orientation latency

2.11.1.1 Experiment 1

Figure S2.1 shows the mean orientation latency for each trial type in all experiments. None of the interaction, the main effect of the trial type, and the main effect of the boundary was significant, $Fs(1, 62) \leq 1.18$, $ps \geq .281$, $\eta_p^2 s \leq 0.02$.

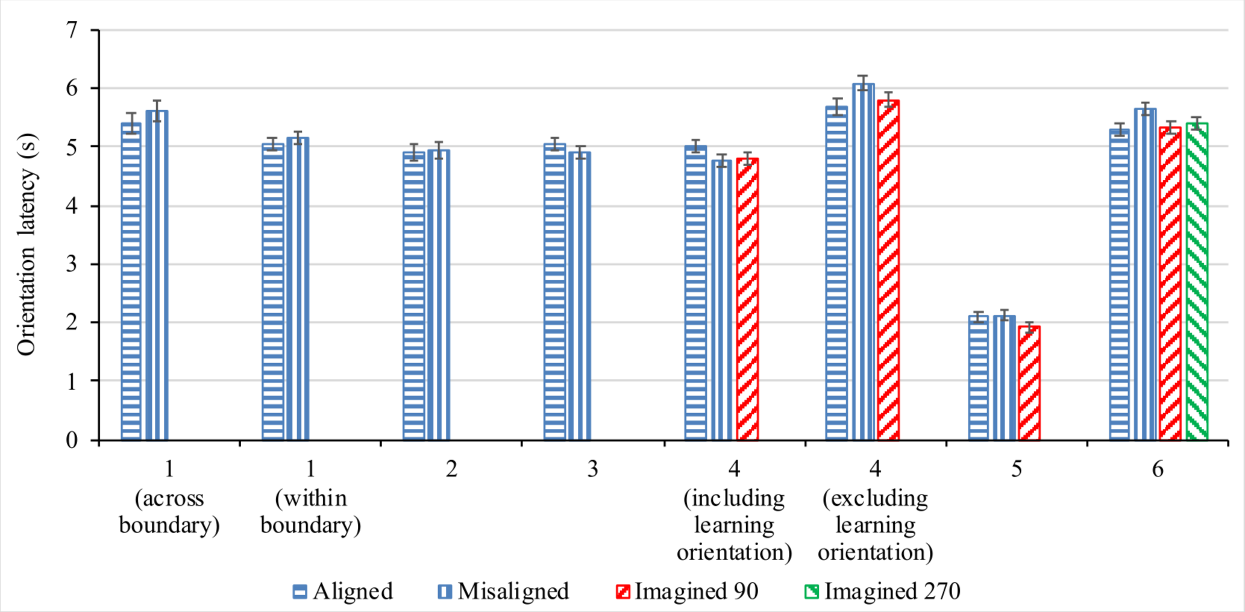

Figure S2.1. The mean orientation latency for each trial type in all experiments. Error bars represent ±1 SE removing the variance from individual differences.

2.11.1.2 Experiment 2

The responses in the aligned trials were not different from those in the misaligned trials, $t(31) = 0.20$, $p = .845$, Cohen's $d = 0.05$.

2.11.1.3 Experiment 3

The responses in the aligned trials were not different from those in the misaligned trials, $t(31) = 0.98$, $p = .334$, Cohen's $d = 0.25$.

2.11.1.4 Experiment 4

The main effect of trial type was not significant, $F(2, 124) = 0.65$, $p = .524$, $\eta_p^2 = 0.01$. The main effect of learning orientation was significant, $F(1, 62) = 8.22$, $p = .006$, $\eta_p^2 = 0.12$, showing that the orientation latency was faster in the group with the learning orientation included in the testing imagined perspectives than in the group with the learning orientation excluded. The interaction between learning orientation and trial type was significant, $F(2, 124) = 3.91$, $p = .022$, $\eta_p^2 = 0.06$. The repeated measures ANOVA were conducted for each group respectively. However, the main effect of trial type was not significant for either group (for the group with the learning orientation included: $F(2, 62) = 1.77$, $p = .180$, $\eta_p^2 = 0.05$; for the group with the learning orientation excluded: $F(2, 62) = 2.57$, $p = .085$, $\eta_p^2 = 0.08$).

2.11.1.5 Experiment 5

The main effect of trial type was not significant, $F(2, 62) = 1.48$, $p = .236$, $\eta_p^2 = 0.05$.

2.11.1.6 Experiment 6

The main effect of trial type was not significant, $F(3, 93) = 2.36$, $p = .077$, $\eta_p^2 = 0.07$.

Chapter 3 Structural Similarity of Local Spaces in a Multiscale Environment Overshadows Global Spatial Representations

3.1 Abstract

This study examined whether and how the structural similarity of local spaces interferes with updating navigators' global headings in a novel multiscale environment. In an immersive virtual environment, the participants learned objects' locations in one room. Then they were blindfolded and physically walked to a neighbouring room for testing. The learning and testing rooms were both rectangular but globally misaligned (one north-south oriented and the other east-west oriented). Adopting different physical perspectives in the testing room, the participants judged relative directions (JRDs) from the imagined perspectives in the learning room. Sensorimotor alignment effects (i.e., performances were better when the imagined perspectives and the physical perspectives were aligned rather than misaligned) were examined when the alignment was defined by the local room structures and when the alignment was defined by global cardinal directions. Prior to JRDs, the participants did not conduct other tasks (Experiment 1), conducted the relative heading judgment between two views in different rooms while seeing the testing room (Experiment 2), or conducted the relative heading judgment in darkness (Experiment 3). The local sensorimotor alignment effect appeared in all experiments. The global sensorimotor alignment effect appeared only in Experiment 3. These results suggest that the structural similarity of local spaces interferes with updating navigators' global headings in the multiscale environment and that this interference occurs during rather than after the activation of global representations by the relative heading judgment.

Keywords*:* sensorimotor alignment effect; structural similarity; spatial representations; spatial updating; multiscale environment

3.2 Introduction

During navigation, people update their self-location (i.e., their headings and positions) based primarily on two methods, piloting and path integration. Piloting relies on visual cues, such as familiar landmarks, to update self-location (Cheng & Spetch, 1998; Etienne, Maurer, Boulens, Levy, & Rowe, 2004; Foo, Warren, Duchon, & Tarr, 2005; Wehner, Michel, & Antonsen, 1996). By contrast, path integration relies on self-motion cues, such as optic flow and idiothetic cues (e.g., vestibular, proprioceptive, motor efference information) during physical movement, to continually update self-location (Etienne & Jeffery, 2004; Loomis, Klatzky, Golledge, & Philbeck, 1999; Mittelstaedt & Mittelstaedt, 1980; Wang, 2017). These two methods are not only applicable to updating self-location during navigation in an immediate space (e.g., Cheng, 1986; Doeller & Burgess, 2008; Klatzky, Loomis, Beall, Chance, & Golledge, 1998; Mou, McNamara, Valiquette, & Rump, 2004; Rieser, 1989; Waller, Montello, Richardson, & Hegarty, 2002), but are also applicable to updating self-location when navigating between different spaces in a multiscale environment (Kelly, Avraamides, & Loomis, 2007; Lei & Mou, under review; Riecke & McNamara, 2017).

In a multiscale environment with several across-boundary spaces (e.g., a building with several offices), people navigate within a space (e.g., within an office) and develop local representations for spatial relations within a space (e.g., locations within an office), and they also navigate between spaces across boundaries (e.g., between different offices) and develop global representations for spatial relations between local spaces (e.g., locations in different offices) (Han & Becker, 2014; Lei, Mou, & Zhang, 2020; Shine, Valdés-Herrera, Hegarty, & Wolbers, 2016; but see Marchette, Vass, Ryan, & Epstein, 2014). When people navigate in a multiscale environment, they see minimal visual cues outside the boundary of the immediate space to directly perceive spatial relations between spaces across boundaries. Thus, when navigating from a remote space to an immediate space across boundaries, people primarily rely on self-motion cues (i.e., path integration) to develop a global spatial representation of the multiscale environment and update their self-location in the global representations. For example, when people move from office A to office B with their eyes closed, self-motion cues can update their self-location in the global representations of both offices. This means of updating based on path integration in across-boundary navigation is referred to as *global-path-integration* (Lei & Mou, under review). It is a prevailing theoretical claim that *global-path-integration* is the primary means to develop global spatial representations (Gallistel, 1990; Jacobs & Schenk, 2003; Loomis et al., 1999; McNaughton, Battaglia, Jensen, Moser, & Moser, 2006; Meilinger, 2008).

However, empirical evidence has shown that it is difficult to develop global spatial representations of a multiscale environment using *global-path-integration* (Lei et al., 2020; Marchette, Ryan, & Epstein, 2017; Marchette et al., 2014). Some studies have shown that people only encode spatial relations within local spaces, but do not encode global spatial relations across spaces (Brockmole & Wang, 2002; Marchette et al., 2014). Other studies have shown that there may be some preconditions to develop global representations, such as explicit instructions to encode global relations (Shine et al., 2016), or some prior learning of the global environment (Lei et al., 2020). These studies suggest that it is difficult to develop global spatial representations using *global-path-integration*. Researchers have attributed this difficulty to the minimal visual information in across-boundary navigation (Mou & Wang, 2015), to the error-prone nature of path integration (Etienne & Jeffery, 2004), and to the disengagement from spatial updating in remote spaces when people move in the immediate space (Wang, 2016). In the current study, we investigate whether, in addition to these reasons, the misaligned but structurally similar local spaces used in previous studies (e.g., Marchette et al., 2014) also contribute to the difficulty in developing global representations of a multiscale environment using *global-path-integration.*

Although people cannot directly see a remote space in a multiscale environment, they can re-anchor themselves in the remote space based on the visual similarity of structures in the immediate and the remote spaces (Riecke & McNamara, 2017). For example, suppose offices A and B have the same rectangular structure with a window on one short wall. In such a case, facing the window in office B would re-anchor people to face the window in office A. In Riecke and McNamara (2017), the participants learned objects' locations in one room and then were disoriented and led to another room for testing. The testing room shared a similar structure with the learning room but contained no original objects. The participants performed a judgment of relative direction (JRD) task in which they mentally adopted perspectives and pointed to target objects ("imagine standing at object A and facing object B, point to object C") in the learning room. The results showed better performances when the imagined perspectives in the learning room and the physical perspectives in the testing room were aligned in terms of local room structures (e.g., imagining facing the door in the learning room while physically facing the door in the testing room) than when they were misaligned. This sensorimotor alignment effect suggests that people who do not develop any global spatial representations can update self-location relative to a remote space based on local structural similarity between the immediate and remote spaces. When the imagined perspective and the re-anchored perspective in the remote space are misaligned, sensorimotor interference occurs, generating sensorimotor alignment effects (Avraamides & Kelly, 2008; Kelly et al., 2007; Riecke & McNamara, 2017; Shelton & Marchette, 2010). This means of updating based on local structural similarity is referred to as *visual re-anchoring* (Lei & Mou, under review). Note that *visual re-anchoring* relies on recognizing familiar visual information to update self-location, so the current study regards *visual re-anchoring* as an instance of piloting.

Hence, after people navigate between spaces across boundaries, they can update self-location relative to a remote space via both *global-path-integration* and *visual re-anchoring*. When the local spaces are structurally similar but the principal axes of the spaces are globally misaligned (e.g., Marchette et al., 2014), *visual re-anchoring* and *global-path-integration* will produce conflicting estimates of self-location. The findings in cue combination literature suggest that people may prefer visual cues (i.e., piloting) over self-motion cues (i.e., path integration) when these two cues produce conflicting spatial estimates (Etienne et al., 2004; Foo et al, 2005; Zhang & Mou, 2017; Zhao & Warren, 2015). In addition, some studies have shown that in homing behaviours, piloting and path integration may interact to determine the navigator's self-location prior to determining the home location (e.g., Zhang, Mou, Lei, & Du, 2019). Furthermore, *visual re-anchoring* relies on visual cues in the local space that are always visually available, whereas *global-path-integration* relies on self-motion cues during across-boundary navigation that may decay after arriving at the destination (e.g., Mou & Zhang, 2014; Zhang & Mou, 2017). When the updated self-locations from these two means are not consistent, *visual re-anchoring* may play a dominant role over *global-path-integration*. Therefore, we propose the first hypothesis regarding the relations between *visual re-anchoring* and *global-path-integration* in updating self-location in a multiscale environment. *Visual re-anchoring* interferes with *global-path-integration*. We refer to this hypothesis as the interference hypothesis.

The interference hypothesis is partially supported by two recent studies showing that global spatial updating occurs more easily when *visual re-anchoring* cannot interfere with *global-path-integration* (Chapter 2) than when *visual re-anchoring* may interfere with *global-path-integration* (Lei & Mou, under review). In particular, in Lei and Mou (under review), the participants learned an environment with two rooms by navigating within and between the rooms. The two rooms were structurally the same (i.e., rectangular rooms with a window on one short wall) but faced different global (cardinal) directions with an angular difference of 90°. The participants had developed local and global representations of the multiscale environment after extensive across-boundary navigation before testing (Lei et al., 2020). During testing, the participants navigated to adopt a physical view in one room (i.e., physical perspective) and did a JRD trial in which they mentally adopted a view (i.e., imagined perspective) in the other room. The results constantly showed local sensorimotor alignment effects, which were attributed to *visual re-anchoring* (Riecke & McNamara, 2017). However, the global sensorimotor alignment effects (i.e., better performances when physical and imagined perspectives faced the same cardinal direction) only occurred when the participants did a global-relevant task (judging relative global headings of two views from different rooms) to activate the global representations prior to the JRD task. Thus, when the two local spaces were globally misaligned and structurally similar, the global sensorimotor alignment effects occurred only when the participants had developed global spatial representations after extensive learning and the global representations were activated on the sensorimotor level by global-relevant tasks.

By contrast, in Chapter 2, the participants learned objects in one square room and then had one-time navigation from this square room to another square room to conduct the JRD task. The participants adopted mental perspectives in the original square room. Since the local geometry of a square was not decisively informative to determine self-location, the participants could update self-location relative to the original square room primarily by *global-path-*

integration. The results from the JRD task showed global sensorimotor alignment effects constantly in all six experiments, providing strong evidence that the participants developed global representations and updated headings in the global representations by one-shot across-boundary navigation. These findings significantly differed from the findings of Lei and Mou (under review, see also Lei et al., 2020; Marchette et al., 2017; Marchette et al., 2014; Shine et al., 2016). The differences in the findings could be due to the fact that the square rooms were used in the experiments of Chapter 2 but the globally misaligned rectangular rooms were used in Lei and Mou (under review). *Visual re-anchoring* might have overshadowed *global-path-integration* in Lei and Mou (under review), thus supporting the interference hypothesis.

However, there are other procedural differences between these two studies (Lei & Mou, under review, Chapter 2), which might also explain the appearance and disappearance of the global sensorimotor alignment effects. Critically, the experiments in Chapter 2 allowed the participants to physically walk during across-boundary navigation, thus enabling full-body movement with physical rotation and physical translation. By contrast, Lei and Mou (under review, see also Lei et al., 2020; Shine et al., 2016) used immersive virtual environments which allowed only physical rotation but visual translation during across-boundary navigation. Similarly, other studies that showed difficulty in developing global spatial representations of two misaligned rooms used desktop virtual environments which provided only visual translation and visual rotation during navigation (Marchette et al., 2017; Marchette et al., 2014).

Thus, the difficulty in developing global representations of structurally similar but globally misaligned spaces (e.g., Lei & Mou, under review; Marchette et al., 2014) might be caused by the lack of full idiothetic cues in path integration during navigation rather than the interference from *visual re-anchoring*. The importance of idiothetic cues on path integration and navigation has been demonstrated by previous studies (Chance, Gaunet, Beall, & Loomis, 1998; Klatzky et al., 1998; Rieser, 1989; Taube, Valerio, & Yoder, 2013). In large-scale environments, body-based cues from active movement benefit spatial knowledge of directions (Waller, Loomis, & Haun, 2004). Idiothetic cues from physical translation may be more crucial than those from physical rotation to acquire spatial knowledge of directions and distances in large-scale environments (Ruddle, Volkova, & Bülthoff, 2011). The lack of idiothetic cues for physical translation and/or physical rotation during navigation may affect the function of path integration to develop global representations and update self-location relative to global relations (Lei & Mou, under review; Lei et al., 2020; Marchette et al., 2017; Marchette et al., 2014).

Therefore, we proposed the second hypothesis about the relations between *visual re-anchoring* and *global-path-integration. Global-path-integration* functions independently from *visual re-anchoring*. *Visual re-anchoring* does not interfere with developing global representations and updating self-location in the global representations using *global-path-integration* when people navigate between two globally misaligned but structurally similar spaces. The difficulty in developing global representations and updating self-location by *global-path-integration* reported in the previous studies (Lei & Mou, under review; Lei et al., 2020; Marchette et al., 2017; Marchette et al., 2014) was attributed to the lack of full idiothetic cues during across-boundary navigation. When navigating with full-body movement, people update self-location in global representations of the spaces, in addition to updating self-location based on local structural similarity. We refer to this hypothesis as the independence hypothesis.

The independence hypothesis may be supported by the fact that *visual re-anchoring* and *global-path-integration* function on different environmental scales. *Visual re-anchoring* relies on structures in local spaces and updates self-location in local representations, whereas *global-path-*

integration relies on global relations between spaces and updates self-location in global representations. It is possible that these two means do not interact because they update self-location in different spatial representations of environmental scales. Furthermore, some studies have assumed that piloting and path integration are independent navigation systems and they generate independent goal estimates (Chen, McNamara, Kelly, & Wolbers, 2017; Chen, Vieweg, & Wolbers, 2019), supporting the independence hypothesis.

The current study tested the interference hypothesis and the independence hypothesis when people have one-shot navigation in multiscale environments. Differentiating these two hypotheses will significantly advance our understanding of the roles of visual and self-motion cues in updating self-location and developing global spatial memory in multiscale environments. Experiment 1 was designed to test the interference hypothesis and the independence hypothesis. As the results of Experiment 1 supported the interference hypothesis, Experiments 2 and 3 were then designed to further understand the mechanism through which *visual re-anchoring* interferes with *global-path-integration*.

3.3 Experiment 1

The purpose of Experiment 1 was to test the interference hypothesis and the independence hypothesis. The experimental setup and procedures in Experiment 1 were the same as for the experiments in Chapter 2; they constantly showed global sensorimotor alignment effects, except that *visual re-anchoring* could occur in the current experiment. Instead of using two square rooms as in Chapter 2, Experiment 1 used two rectangular rooms with globally misaligned principal axes, creating inconsistent updated headings according to *visual re-anchoring* and *global-path-integration*. The participants learned objects' locations in one room, and then were blindfolded and led to walk to the other adjacent room. During testing, while they were facing physical perspectives in the testing room, they conducted the JRD task in which they adopted imagined perspectives and then pointed to target objects in the learning room. In the JRD task, the imagined perspectives in the learning room and the physical perspectives in the testing room were manipulated to be globally/locally aligned/misaligned, to examine global/local sensorimotor alignment effects. Following the interference hypothesis, there would be a local sensorimotor alignment effect based on *visual re-anchoring* but no global sensorimotor alignment effect based on *global-path-integration*, whereas following the independence hypothesis, there would be both global and local sensorimotor alignment effects as *global-path-integration* and *visual re-anchoring* function independently.

3.3.1 Method

3.3.1.1 Participants

The study was approved by the Ethics Committee of the University of Alberta. Thirty-two university students (16 females) with normal or corrected-to-normal vision participated for credits in an introductory psychology course. This number of participants was the same as in the experiments of Chapter 2.

3.3.1.2 Materials and design

In the real lab space, there were two lab rooms (4.4 m × 4.4 m each) and a hallway (Figure 3.1A). In each real lab room, an immersive virtual environment was generated by Vizard software (WorldViz, Santa Barbara, CA) and was presented in a head-mounted display (HMD, Oculus Rift, Oculus VR, LLC., Irvine, CA). Head motion tracking was carried out by an InterSense IS-900 motion tracking system (InterSense, Inc., Massachusetts). The participants physically walked and made turns to move in the virtual environment. In the learning phase, the participants replaced objects using a virtual pointer controlled by an InterSense Wand. In the testing phase, the participants did the JRD task using a joystick (Logitech Extreme 3D Pro, Newark, CA).

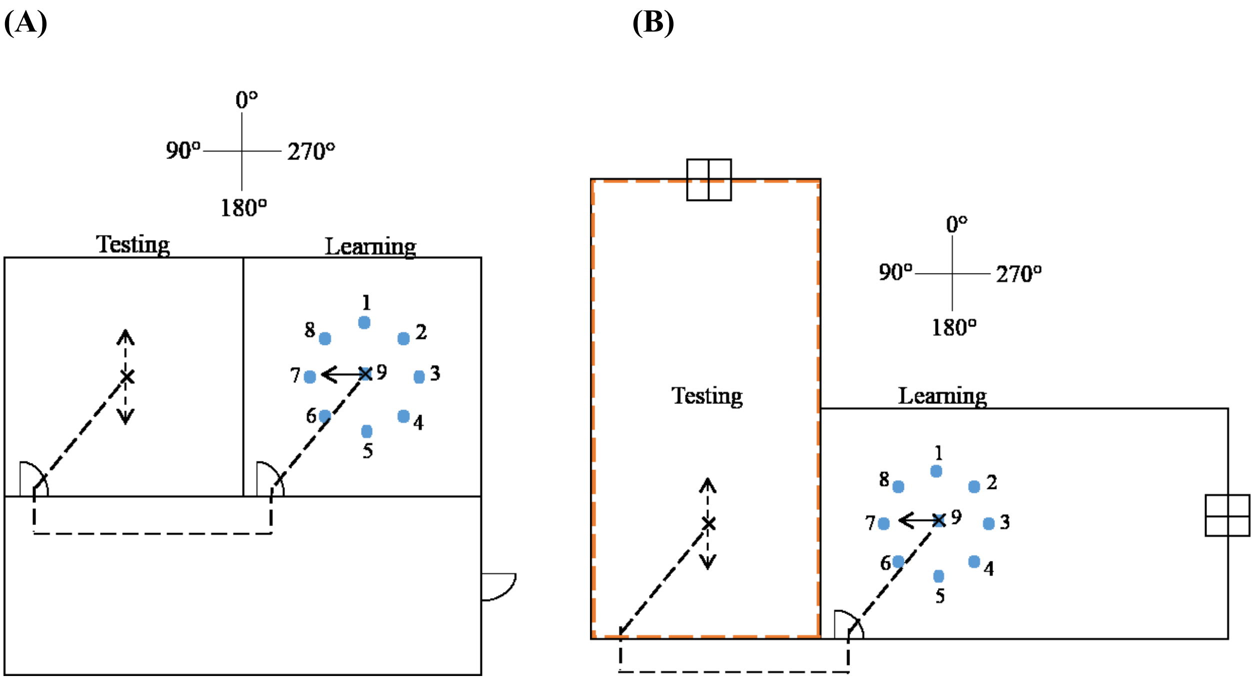

Figure 3. 1 Schematic experimental setup in the current study. (A) A real lab space with two lab rooms and a hallway. (B) Virtual rooms in an immersive virtual environment. The blue dots are objects. The crosses are the learning/testing positions. The solid arrow is the learning orientation (i.e., 90°). The dashed arrows are the physical perspectives in testing (i.e., 0° and 180°). The black dashed lines indicate the walking path from the learning position to the testing position. The red dashed lines along the virtual testing room indicate red walls. The compass indicates the labels for directions used in the current study.

One real lab room was for the learning phase and the other was for the testing phase. The learning and testing positions were at the centers of the real lab rooms. The walking path was from the learning position to the testing position. However, although the participants moved in the real lab space, they never saw the real lab space; they saw only the virtual environments presented in each real lab room (Figure 3.1B). The virtual learning and testing rooms were structurally similar as both virtual rooms were rectangular (4.4 m × 8.8 m each) and had a window on one short wall, yet the virtual rooms were in different colors and textures. The principal axes and the orientations of the windows in the two virtual rooms were globally 90° apart so that the virtual learning and testing rooms were globally misaligned. In addition, the virtual learning room had a door, which overlapped with the door in the real lab room for learning, whereas the virtual testing room did not have a door. The virtual rooms were partially superimposed onto the real lab rooms. In particular, the left wall in the virtual learning room overlapped with the left wall in the real lab room for learning, whereas the bottom wall in the virtual testing room overlapped with the bottom wall in the real lab room for testing. Thus, the left half of the virtual learning room overlapped with the real lab room for learning, whereas the bottom half of the virtual testing room overlapped with the real lab room for testing.

In the learning phase, the participants learned locations of objects placed on the ground in the virtual learning room while standing at object 9 and facing object 7 (Figure 3.1). Eight objects formed a circular array (radius=1.8 m) in which the adjacent locations were 45° apart and one object was in the center of the circle (object 9, which was also the learning position). To increase the reality of the virtual environment, there were real objects placed at the same locations on the ground in the real lab room for the participants to touch.

The global and local alignments were independently manipulated in the JRD trials and were within-subject variables. The participants physically faced different perspectives in the testing room while doing JRDs. The physical perspectives in the testing room were 0° and 180°, and the imagined perspectives in the learning room were 0°, 90°, 180° and 270° (Figure 3.1). Together, they formed globally/locally aligned/misaligned conditions (see Table 3.1). In the globally aligned/misaligned conditions, the physical and imagined perspectives were aligned/misaligned in terms of the global cardinal directions. For example, if the imagined perspective was 0°, then the physical perspective was also 0° in the globally aligned condition but was 180° in the globally misaligned condition. In the locally aligned/misaligned conditions, the physical and imagined perspectives were aligned/misaligned in terms of the local structures. For example, if the imagined perspective in the learning room was facing the window (270°), then the physical perspective in the testing room was also facing the window (0°) in the locally aligned condition but was facing the opposite wall of the window (180°) in the locally misaligned condition. The contrast between the globally aligned and globally misaligned conditions examined the global sensorimotor alignment effect, and the contrast between the locally aligned and locally misaligned conditions tested the local sensorimotor alignment effect. Note that in the globally (locally) aligned/misaligned conditions, the angular distance between the physical and imagined perspectives was locally (globally) 90° so that the global and local sensorimotor alignment effects did not confound each other. The dependent measures were the response latency and absolute pointing error in the JRD trials.

The JRD trials were blocked by the two physical perspectives (i.e., 0° and 180°). In each block, 16 trials were generated for each of the four imagined perspectives, leading to 64 trials (see Table 2.3 in Chapter 2, for the standing, facing and target objects used for the four imagined perspectives). The trials were randomized in each block. The order of the two blocks was counterbalanced across the participants.

Table 3. 1 Imagined and physical perspectives in four conditions of the JRD task (i.e., globally/locally aligned/misaligned). The directions of the perspectives refer to Figure 3.1.

Conditions		Imagined perspectives			
		0°	180°	270°	90°
Physical perspectives	0°	Globally aligned	Globally misaligned	Locally aligned	Locally misaligned
	180°	Globally misaligned	Globally aligned	Locally misaligned	Locally aligned

3.3.1.3 Procedure

Before the formal experiment, the participants signed consent forms, read instructions and practiced using the joystick. Then the participants were blindfolded and guided to the real lab room for learning. The participants were led to stand at the learning position (i.e., object 9 in Figure 3.1) and face the learning orientation (i.e., facing object 7 which was 90°, indicated by the solid arrow in Figure 3.1). They closed their eyes, removed the blindfold and put on the HMD.

The participants saw the virtual learning room. To familiarize the room, they looked around and also walked to touch the real wall in front of them (i.e., the left wall in the learning room in Figure 3.1). Then the participants returned to the learning viewpoint (i.e., standing at object 9 and facing object 7 in Figure 3.1), and the objects were presented. The participants named the objects with the help of the experimenter. After that, instructed by the experimenter, the participants moved to touch three real objects on which the virtual objects were superimposed (object 7 in the front, object 6 on the walking path later on, a third random object in Figure 3.1). To touch each object, the participants moved from the learning position and went back after touching. Moving to touch the wall and the objects helped the participants calibrate their physical movement in the virtual environment and realize that the virtual environment was as stable as the real environment (Mohler, Creem-Regehr, & Thompson, 2006; Siegel, Kelly, & Cherep, 2017; Taube et al., 2013). Then the participants returned to the learning viewpoint to learn the object's locations for three minutes. After that, the objects were removed and a probed object with its name appeared at the center of the HMD. The participants used a virtual pointer to replace the probed object. The probed object was then presented at the response location and also at the correct location as feedback. The participants replaced the objects in three blocks, with the objects randomly tested in each block. After that, the objects were presented. When the participants notified the experimenter that they had memorized the objects' locations, the objects were removed and the learning phase was finished.

Before the testing phase, the participants went through some procedures to make them further realize that the objects were stabilized relative to the environment rather than their bodies during navigation (Mou, Li, & McNamara, 2008). After the learning phase, the participants returned to the learning viewpoint (standing at object 9 and facing object 7 in Figure 3.1). They closed their eyes, took off the HMD and put on the blindfold. At the learning viewpoint, the participants were instructed to use their fingers and point to some objects that were randomly named by the experimenter. Then they were instructed to turn and face object 6 (Figure 3.1). They used their fingers to point to some objects randomly named by the experimenter. After that, they closed their eyes to remove the blindfold and put on the HMD. They saw the virtual environment from the new viewpoint (i.e., standing at object 9 and facing object 6 in Figure 3.1) and replaced all the objects at the original locations. Each object was tested once without feedback. Then the participants closed their eyes to take off the HMD and put on the blindfold. They were led to walk from object 9 to object 6 (Figure 3.1). Again, they used their fingers to point to some objects and then put on the HMD to replace all the objects from the new viewpoint (standing at object 6 and facing the walking direction from object 9 to object 6 in Figure 3.1). Seeing the virtual environment from new viewpoints helped the participants realize that the virtual environment was stable just like the real environment. Replacing the objects from new viewpoints helped the participants realize that the objects were stable in the virtual environment and were not moving along with their bodies.

Then the participants closed their eyes to take off the HMD and put on the blindfold. Prior to walking to the testing position, the participants were instructed that they would walk to another room and should pay attention to the walking and track the objects. Before leaving the learning room, the participants touched the door of the learning room to ensure that they would walk outside. The participants were guided to the testing position along the walking path (the black dashed lines in Figure 3.1) and oriented to face one physical perspective (0° or 180°, the dashed arrows in Figure 3.1). The participants were told that they had walked into a new room.

In the testing room, the participants put on the HMD and saw a new room. They conducted the first block of the JRD trials after facing the first physical perspective. In the JRD trial, a sentence to instruct an imagined perspective was shown at the center of the HMD (e.g., "standing at the bottle, facing the paperclip"). If the participants adopted the imagined perspective, they clicked the trigger on the joystick and the sentence disappeared. The duration between the appearance of the imagined perspective and the clicked trigger was recorded as orientation latency. Then another sentence was shown to instruct a target object (e.g., "point to the mug"). The participants pointed to the target from the imagined perspective. They were required to point as fast as possible without sacrificing accuracy. The sentence disappeared after pointing. The duration between the appearance of the target and the pointing response was recorded as response latency. The response pointing direction was recorded and was compared with the correct direction to get the absolute angular pointing error. The intertrial interval was 750 ms. The participants finished the first block of the JRD trials and then they were turned to the other physical perspective to finish the second block.

3.3.1.4 Data analysis

For each of the four conditions (i.e., globally/locally aligned/misaligned), we calculated the mean orientation latency, mean response latency and mean absolute angular pointing error. To test the global/local sensorimotor alignment effects, paired-sample *t* tests were conducted to compare performances between globally/locally aligned and globally/locally misaligned conditions. To qualify any null effect, we also calculated the Bayes factor favoring the null effect over the alternative effect (BF_{01})[3].

3.3.2 Results

The results from orientation latency were not significant in all experiments of the current study (Figure S3.1 in the supplementary materials). Thus, the detailed results from response latency and absolute pointing error were reported as follows.

3.3.2.1 Response latency

Figure 3.2 plots the mean response latency for each condition in all experiments. The response latency in the globally aligned condition was not significantly different from that in the globally misaligned condition, $t(31) = 1.21$, $p = .234$, Cohen's $d = 0.30$, $BF_{01} = 3.62$, indicating a null global sensorimotor alignment effect.

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[3] The null effect is favored if the BF_{01} is larger than three, and strongly favored if the BF_{01} is larger than 10. The alternative effect is favored if the BF_{01} is smaller than 1/3, and strongly favored if the BF_{01} is smaller than 1/10 (Rouder, Speckman, Sun, Morey, & Iverson, 2009). If the BF_{01} is between 1/3 and three, neither is favored.

The responses in the locally aligned condition were significantly faster than those in the locally misaligned condition, $t(31) = 5.26$, $p < .001$, Cohen's $d = 1.32$, indicating a local sensorimotor alignment effect.

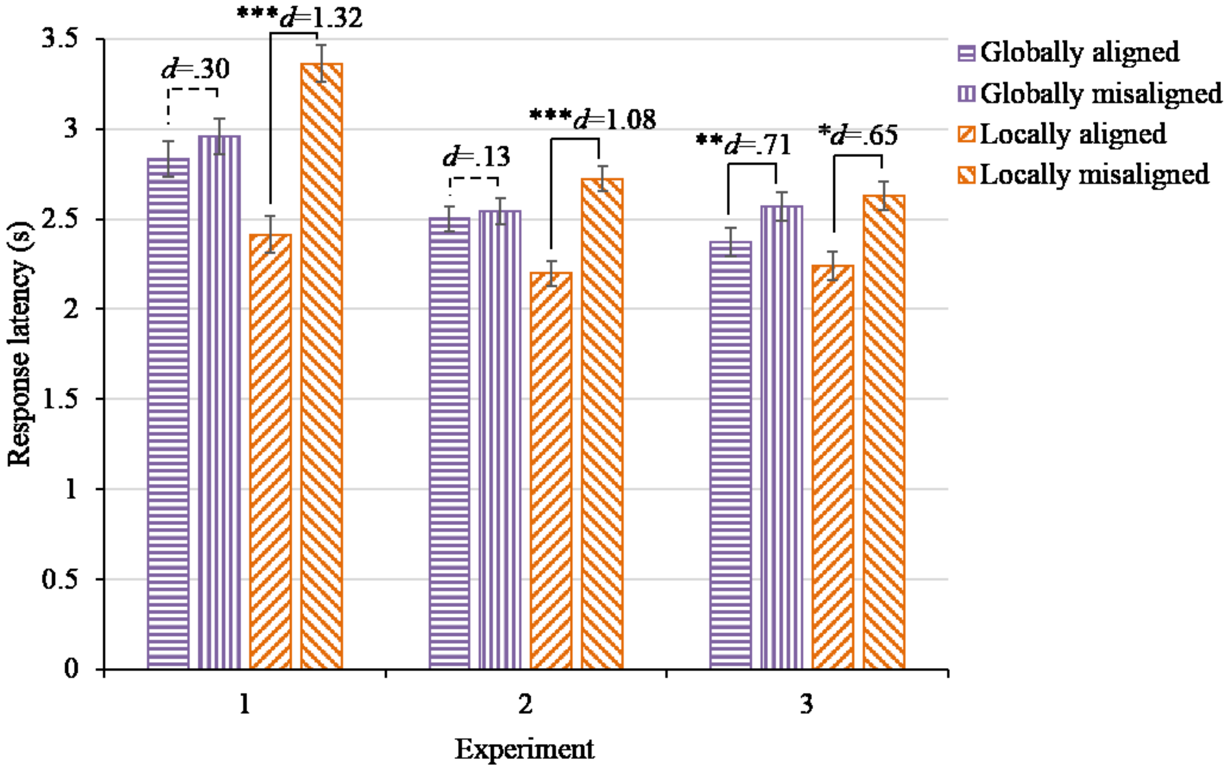

Figure 3. 2 The mean response latency for each condition in all experiments. Error bars represent ±1 SE removing the variance from individual differences. The solid lines indicate significant comparisons, and the dashed lines indicate insignificant comparisons. Cohen's d values are listed (p< .05; ** p< .01; *** p< .001).*

3.3.2.2 Absolute pointing error

Figure 3.3 shows the mean absolute angular pointing error for each condition in all experiments. The absolute pointing error in the globally aligned condition was not significantly different from that in the globally misaligned condition, *t*(31) = 0.71, *p* = .483, Cohen's *d* = 0.18, BF_{01}= 5.72, indicating a null global sensorimotor alignment effect.

The responses in the locally aligned condition were significantly more accurate than those in the locally misaligned condition, *t*(31) = 3.10, *p* = .004, Cohen's *d* = 0.77, indicating a local sensorimotor alignment effect.

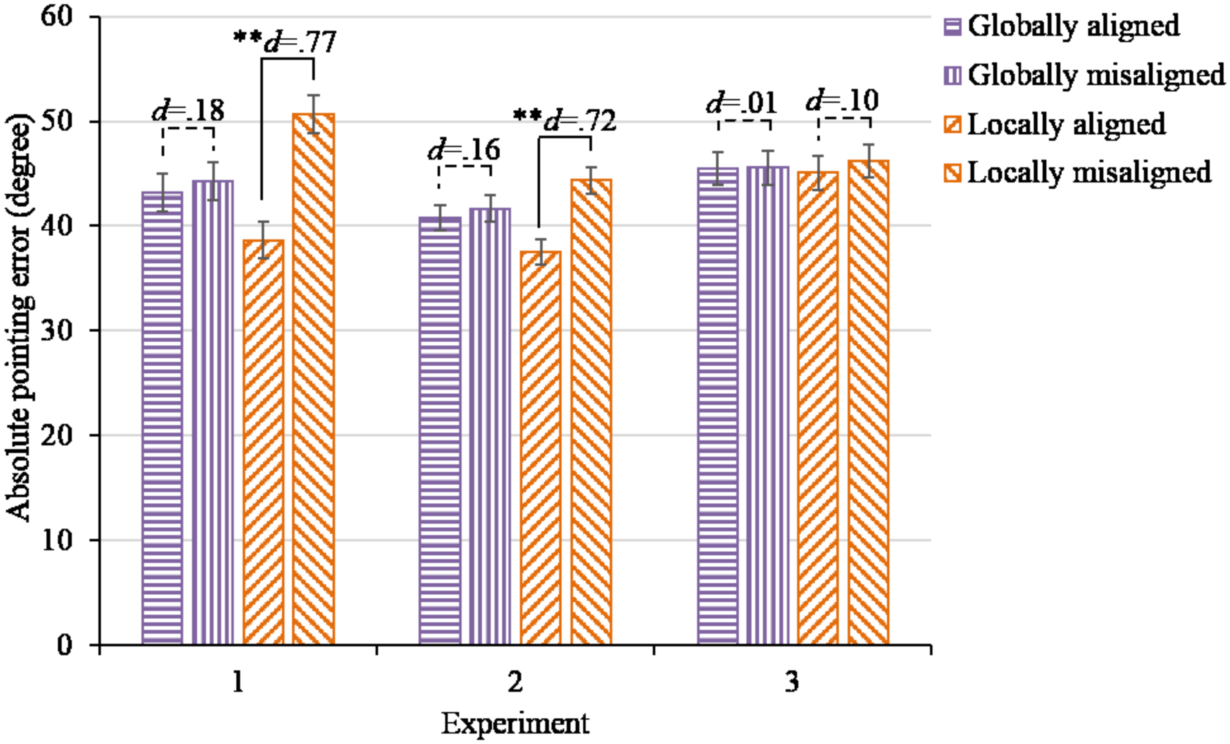

*Figure 3. 3 The mean absolute pointing error for each condition in all experiments. Error bars represent ±1 SE removing the variance from individual differences. The solid lines indicate significant comparisons, and the dashed lines indicate insignificant comparisons. Cohen's d values are listed (** p< .01).*

3.3.3 Discussion

Experiment 1 showed only local sensorimotor alignment effects, indicating that after one-shot walking from the learning to the testing room, the participants only updated their headings relative to the learning room by *visual re-anchoring*. The experiments in Chapter 2 showed robust global sensorimotor alignment effects by one-shot across-boundary walking in all six experiments when there was no local structural similarity to indicate local headings. In particular, Experiment 6 of Chapter 2 was identical to Experiment 1 of the current study except that two square rooms were used in the former and two misaligned rectangular rooms were used in the latter. Therefore, the null global sensorimotor alignment effect in Experiment 1 of the current study suggests that structural similarity and global misalignment between local spaces interfered with updating the participants' headings in the global representations of the two rooms after one-shot across-boundary walking. This result supports the interference hypothesis.

Because the procedures in the current experiment were the same as those in Experiment 6 of Chapter 2 before the testing room was presented, the participants in the current experiment should have developed some global spatial representations during across-boundary walking before they saw the structurally similar but globally misaligned testing room. We speculate that the participants in the current experiment did not utilize global spatial representations in self-localization after seeing the testing room for the following reason: the local self-localization representations associated with *visual re-anchoring* are primary representations on the sensorimotor level whereas the global self-localization representations associated with *global-path-integration* are secondary representations on the sensorimotor level (Lei & Mou, under review; Wang, 2016). Thus, *visual re-anchoring* overshadows *global-path-integration* by prioritizing the local spatial representations (and deprioritizing the global spatial representations) on the sensorimotor level. Experiment 2 tested this possibility.

3.4 Experiment 2

Previous studies have shown that relative heading judgments can activate global representations and bring them onto the sensorimotor level (Burte & Hegarty, 2004; Lei & Mou, under review; Sholl, Kenny, & DellaPorta, 2006). In those studies, relative heading judgments involved participants in the testing room being asked, for example, to face the global direction of a probed view in the learning room. Inspired by these findings, Experiment 2 added a relative heading judgment prior to the JRD trials. If *visual re-anchoring* overshadows *global-path-integration* by prioritizing the local spatial representations (and deprioritizing the global spatial representations) on the sensorimotor level, then the interference will disappear when the global spatial representations are activated by the relative heading judgment, producing global sensorimotor alignment effects in the JRD task following the relative heading judgment.

3.4.1 Method

3.4.1.1 Participants

Thirty-two university students (16 females) with normal or corrected-to-normal vision participated for credits in an introductory psychology course.

3.4.1.2 Materials and design

The virtual environments and the JRD trials were the same as in Experiment 1.

There was one trial in the relative heading judgment task. The participants were asked to turn and face the cardinal direction of the original learning orientation in the virtual learning room (standing at object 9 and facing object 7 in Figure 3.1, which was an allocentric direction of 90°). The participants did one trial of relative heading judgment only from the first physical perspective of the JRD task (either 0° or 180°).

3.4.1.3 Procedure

The learning phase and the walking procedure were the same as in Experiment 1. In the testing phase, after the participants put on the HMD and saw themselves in the testing room, they did one trial of the relative heading judgment. A sentence was presented at the center of the HMD to instruct the probed direction ("Imagine the experimenter is standing at the brush, facing the clock. Turn to face the same direction." Note that the brush was object 9 and the clock was object 7 in Figure 3.1). The participants were instructed to physically turn to face the cardinal direction of the probed direction, and they were allowed to take their time to think. They notified the experimenter after responding and the experimenter pressed a key on the keyboard to record the participants' facing direction (recorded by the motion tracker on the HMD). The sentence on the HMD disappeared. The participants were turned back to the initial physical perspective (i.e., 0° or 180°), and continued to conduct the JRD task.

3.4.2 Results

The results of the relative heading judgment can be found in the supplementary materials (Figure S3.2A).

3.4.2.1 Response latency

Figure 3.2 plots the mean response latency for each condition. The response latency in the globally aligned condition was not significantly different from that in the globally misaligned condition, $t(31) = 0.53, p = .603$, Cohen's $d = 0.13$, $BF_{01} = 6.38$, indicating a null global sensorimotor alignment effect.

The responses in the locally aligned condition were significantly faster than those in the locally misaligned condition, $t(31) = 4.31, p < .001$, Cohen's $d = 1.08$. This shows a local sensorimotor alignment effect.

3.4.2.2 Absolute pointing error

Figure 3.3 plots the mean absolute angular pointing error for each condition. The absolute pointing error in the globally aligned condition was not significantly different from that in the globally misaligned condition, *t*(31) = 0.66, *p* = .516, Cohen's *d* = 0.16, BF_{01}= 5.92, demonstrating a null global sensorimotor alignment effect.

The responses in the locally aligned condition were significantly more accurate than those in the locally misaligned condition, *t*(31) = 2.89, *p* = .007, Cohen's *d* = 0.72, indicating a local sensorimotor alignment effect.

3.4.3 Discussion

Experiment 2 still showed only local sensorimotor alignment effects as in Experiment 1, even when the participants in Experiment 2 conducted the relative heading judgment prior to the JRD task. Therefore, *visual re-anchoring* overshadows *global-path-integration* not just by prioritizing local spatial representations and deprioritizing global spatial representations on the sensorimotor level (Lei & Mou, under review; Wang, 2016). This finding differs from that in Lei and Mou (under review), which showed the global sensorimotor alignment effect when the participants conducted the relative heading judgment prior to the JRD task. This discrepancy will be addressed in the general discussion of this chapter.

Even though Experiment 2 showed the interference from *visual re-anchoring* on *global-path-integration* in the JRD task following the relative heading judgment, it is not clear whether this overshadowing occurred during the relative heading judgment to activate the global representations onto the sensorimotor level or after the global representations were activated by the relative heading judgment. Experiment 3 tackled this issue.

3.5 Experiment 3

The participants in Experiment 3 conducted the relative heading judgment in darkness without the presentation of the virtual testing room. In this way, it was possible to avoid the interference from local structural similarity so that the relative heading judgment could successfully activate the global relations on the sensorimotor level. If the global sensorimotor alignment effect appeared, then this result would support that the interference from *visual re-anchoring* on *global-path-integration* occurred during rather than after the relative heading judgment which activated global spatial representations onto the sensorimotor level.

3.5.1 Method

3.5.1.1 Participants

Thirty-two university students (16 females) with normal or corrected-to-normal vision participated for credits in an introductory psychology course.

3.5.1.2 Materials, design and procedure

The materials, design and procedure were the same as in Experiment 2, except for the following change in the relative heading judgment task. After the participants were led to the testing position and oriented to the physical perspective, they put on the HMD and saw a dark screen. The participants conducted one trial of relative heading judgment in darkness. After they finished responding, they were turned back to the initial physical perspective. Then the virtual testing room was presented and the participants conducted the JRD task.

3.5.2 Results

The results of the relative heading judgment can be found in the supplementary materials (Figure S3.2B).

3.5.2.1 Response latency

Figure 3.2 plots the mean response latency for each condition. The responses in the globally aligned condition were significantly faster than those in the globally misaligned condition, $t(31) = 2.84$, $p = .008$, Cohen's $d = 0.71$. This shows a significant global sensorimotor alignment effect.

The responses in the locally aligned condition were significantly faster than those in the locally misaligned condition, $t(31) = 2.60$, $p = .014$, Cohen's $d = 0.65$, indicating a significant local sensorimotor alignment effect.

3.5.2.2 Absolute pointing error

Figure 3.3 plots the mean absolute angular pointing error for each condition. The absolute pointing error in the globally aligned condition was not significantly different from that in the globally misaligned condition, $t(31) = 0.03$, $p = .980$, Cohen's $d < 0.01$, $BF_{01}= 7.30$, indicating a null global sensorimotor alignment effect.

The absolute pointing error in the locally aligned condition was not significantly different from that in the locally misaligned condition, $t(31) = 0.39$, $p = .700$, Cohen's $d = 0.10$, $BF_{01}= 6.78$, indicating a null local sensorimotor alignment effect.

3.5.3 Discussion

Experiment 3 showed the global sensorimotor alignment effect in addition to the local sensorimotor alignment effect, suggesting that the participants updated headings by *global-path-integration* in addition to *visual re-anchoring*. These results indicate that the interference from *visual re-anchoring* on *global-path-integration* occurs during rather than after activating global spatial representations on the sensorimotor level. After the global representations were successfully activated onto the sensorimotor level, the sensorimotor global representations were immune to the interference from *visual re-anchoring*. The participants could then update their headings in the global representations with the presence of the testing room in the JRD task.

3.6 General Discussion

The current study examined whether and how structural similarity between local spaces interferes with updating people's headings in the global representations of spaces by one-shot across-boundary walking between the spaces. There are two main findings. First, the globally misaligned and structurally similar local spaces interfered with updating global headings. Second, this interference occurred during rather than after activating the global spatial representations on the sensorimotor level.

To the best of our knowledge, the current study demonstrated, for the first time, that the globally misaligned and structurally similar local spaces interfered with updating global headings. Previous studies have shown the local sensorimotor alignment effects attributed to *visual re-anchoring* and have demonstrated that people can re-anchor themselves in a remote space based on the similar visual structures of the current space and the remote space (Riecke & McNamara, 2017). Previous studies have also shown global sensorimotor alignment effects attributed to *global-path-integration* and have demonstrated that people can update their headings in the global representations of two square rooms by one-shot across-boundary walking between the rooms (see Chapter 2). Lei and Mou (under review) showed both the local sensorimotor alignment effects attributed to *visual re-anchoring* and the global sensorimotor alignment effects attributed to *global-path-integration.* However, before the current study, there was no study testing whether *visual re-anchoring* interferes with *global-path-integration* (interference hypothesis) or that these two means are independent (independence hypothesis). Experiment 1 of the current study was identical to Experiment 6 of Chapter 2 except that the two local spaces were structurally similar but their principal axes were globally misaligned in the former experiment and the two local spaces were square rooms in the latter experiment. The findings that the global sensorimotor alignment effect did not appear in Experiment 1 of the current study but appeared in Experiment 6 of Chapter 2 clearly favor the interference hypothesis over the independence hypothesis.

The finding that *visual re-anchoring* overshadowed *global-path-integration* can explain the difficulty in developing global representations and updating global headings shown in the previous studies. In a multiscale environment containing structurally similar spaces, developing global representations by across-boundary navigation is difficult and requires preconditions such as prior global learning (Lei et al., 2020; Marchette et al., 2017; Marchette et al., 2014). Furthermore, even after people develop global spatial representations, they still need to perform relative heading judgments to bring the global spatial representations onto the sensorimotor level so that they can update global headings (Lei & Mou, under review). Unfortunately, these studies did not enable full-body movement during across-boundary navigation, which confounds with the existence of local structural similarity to explain the difficulty in developing global representations of spaces with similar structures. In the current study, the participants physically walked from the learning position to the testing position, enabling full-body movement during across-boundary navigation. The null global sensorimotor alignment effect in Experiment 1 of the current study indicates that the difficulty in using across-boundary navigation to develop global representations of structurally similar spaces was not necessarily due to the lack of full idiothetic cues in across-boundary navigation, but rather primarily due to the interference from the structural similarity in different local spaces.

Importantly, the current study showed that overshadowing from *visual re-anchoring* on *global-path-integration* occurred during rather than after activating the global spatial representations on the sensorimotor level. In Experiment 2, the participants conducted the relative heading judgment with the testing room presented, prior to the JRD task. The results still showed only local sensorimotor alignment effects. In Experiment 3, the participants conducted the relative heading judgment task without the testing room presented (i.e., in darkness). The results showed that there were both global and local sensorimotor alignment effects. These findings indicate that local structural similarity interferes with activation of the global representations to the sensorimotor level by the relative heading judgment. If global representations are successfully activated to the sensorimotor level, no further interference from local structural similarity occurs in updating self-location in the global representations. This finding provides insight into the mechanism through which *visual re-anchoring* overshadows *global-path-integration.*

The current study shows that the global representations need to be activated by relative heading judgments, to support updating headings in the global representations with the presence of local structural similarity (Experiment 3). This is consistent with the previous finding that the global representations in long-term memory need to be retrieved as sensorimotor global representations in working memory so that people can rely on the global representations to update self-location (Lei & Mou, under review). However, the participants in Experiment 2 also conducted the relative heading judgment prior to the JRD task but Experiment 2 showed no global sensorimotor alignment effect. This result differed from the finding in Lei and Mou (under review), which showed the global sensorimotor alignment effect when the participants conducted the relative heading judgment prior to the JRD task. This discrepancy might be because the participants in Lei and Mou (under review) had extensive across-boundary navigation and prior global learning whereas the participants in the current study had only one-shot across-boundary navigation without any prior global learning.

Some previous studies have shown that extensive navigational experiences may be critical to developing global representations in large-scale environments (Han & Becker, 2014; He, McNamara, Bodenheimer, & Klippel, 2019; Starrett, Stokes, Huffman, Ferrer, & Ekstrom, 2019). Lei et al. (2020) showed that the participants who had extensive across-boundary navigation did not develop global spatial representations unless they had learned the directions of other buildings before traveling between rooms (prior global learning). As the participants in Lei and Mou (under review) had both extensive across-boundary navigation and prior global learning, they should have developed relatively enduring global representations in their long-term memory. Activation of enduring global representations on the sensorimotor level might be resistant to the interference from seeing the structurally similar but globally misaligned testing room. Thus, in Lei and Mou (under review), the global sensorimotor alignment effect occurred when the participants judged relative headings while seeing the structurally similar but globally misaligned testing room prior to JRDs.

In the current study, the participants only had one-time walking experience between the learning and testing rooms in a novel environment. The global representations developed by one-shot across-boundary walking might have been primitive and might not have been enduring. For example, the participants might have encoded the origin of the walking path relative to the learning room and also their self-location relative to the origin of the walking path (homing vector). However, they might not have organized these two representations in the same global representations during across-boundary walking. Consequently, the global representations of relations between the self-location and the learning room were primitive. Extra steps were needed to turn the primitive global representations to relatively enduring global representations. These steps could be invoked by any task that tapped into global spatial relations (e.g., relative heading judgments). However, in Experiment 2 of the current study, seeing the structurally similar but globally misaligned testing room before and during the relative heading judgment might have disrupted the process of developing enduring global representations. As there were no global representations of spatial relations between self-location and the learning room on the sensorimotor level, there was no global sensorimotor alignment effect in the following JRD task. Importantly, the participants in Experiment 3 conducted the relative heading judgment task without the testing room presented (i.e., in darkness). The results showed both global and local sensorimotor alignment effects. Thus, one trial of judging relative headings could turn the primitive global representations into the relative enduring global representations that were immune to the interference from *visual re-anchoring*.

It is still not clear whether extensive across-boundary navigation with full-body movement can lead to the development of enduring global representations that are immune to interference from the structurally similar but globally misaligned testing room. On one hand, the reciprocal interaction between navigation and spatial memory during extensive across-boundary navigation may contribute to developing global representations, and with more navigational experiences, the primitive global representations may become more integrated and mature to support navigation. On the other hand, Lei et al. (2020) showed that global prior learning might be essential to developing global representations. The prior global learning may provide a common global reference system to turn primitive global representations into enduring global representations. Without prior global learning, the primitive global representations may be washed out by *visual re-anchoring* after each across-boundary walk. Consequently, no enduring global representations can be formed regardless of the number of across-boundary walks. Future studies are needed to test whether global sensorimotor alignment effects appear when participants partake in extensive across-boundary walking with full-body movement and conduct the relative heading judgment with the presence of the structurally similar but globally misaligned testing room prior to the JRD trials.

Some previous studies have assumed that piloting and path integration are two different systems and the estimates from these two systems are combined only at homing (Chen et al., 2017; Chen et al., 2019). Other studies have stipulated that piloting and path integration interact in self-localization prior to homing (Zhang et al., 2019). As we stated in the introduction of this chapter, *visual re-anchoring* is an instance of piloting. Therefore, interference from *visual re-anchoring* on *global-path-integration* in updating the participants' headings (Experiments 1 and 2 of the current study) is consistent with the theoretical position that interaction between piloting and path integration occur in self-localization prior to homing. Importantly, no interference occurred after the participants had developed enduring global spatial representations (Experiment 3 of the current study). This might be because the representations used in piloting (*visual re-anchoring*) and those used in path integration (*global-path-integration*) were on different scales (i.e., local and global scales). As the heading estimates are in two different spatial representations, there is no need to combine the estimates (cue combination) or select one of them (cue competition). Hence, we speculate that the interaction between piloting and path integration in estimating self-location occurs in an environment with a single scale but may not occur in a multiscale environment. This speculation is a theoretical insight and needs further empirical investigations. Therefore, the current findings have important theoretical implications on the roles of visual and self-motion cues in updating self-location and developing global spatial memory.

The interference from *visual re-anchoring* on *global-path-integration* is also applicable to daily life experiences. It is common to navigate in a multiscale environment containing several local spaces with similar structures. For example, there may be several structurally similar classrooms in a school building. It is easy to imagine being immersed in another classroom while sitting in one classroom according to the structures of the classrooms, but it appears harder to indicate the global relations between the classrooms. When people move in a multiscale environment containing several local spaces with similar structures, people primarily develop and engage in the local representations rather than global representations (Marchette et al., 2017; Wang, 2016). People cannot directly see the global relations across boundaries (Mou & Wang, 2015). In addition, globally misaligned but locally similar structures interfere with updating self-location globally. All these factors may contribute to our experiences of difficulty in developing and relying on global representations in daily life.

In conclusion, the current study demonstrated that globally misaligned but locally similar structures in local spaces interfere with developing global representations and updating self-location in the global representations, after one-shot across-boundary walking in a novel environment. This interference occurs during activating the global representations on the sensorimotor level. When global-relevant tasks successfully activate global representations on the sensorimotor level, people can develop global representations and update self-location globally with the presence of misaligned local structural similarity.

3.7 References

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3.8 Supplementary materials

3.8.1 Results from orientation latency

Figure S3.1 shows the mean orientation latency for each condition in all experiments. None of the global or local sensorimotor alignment effect was significant in any experiment.

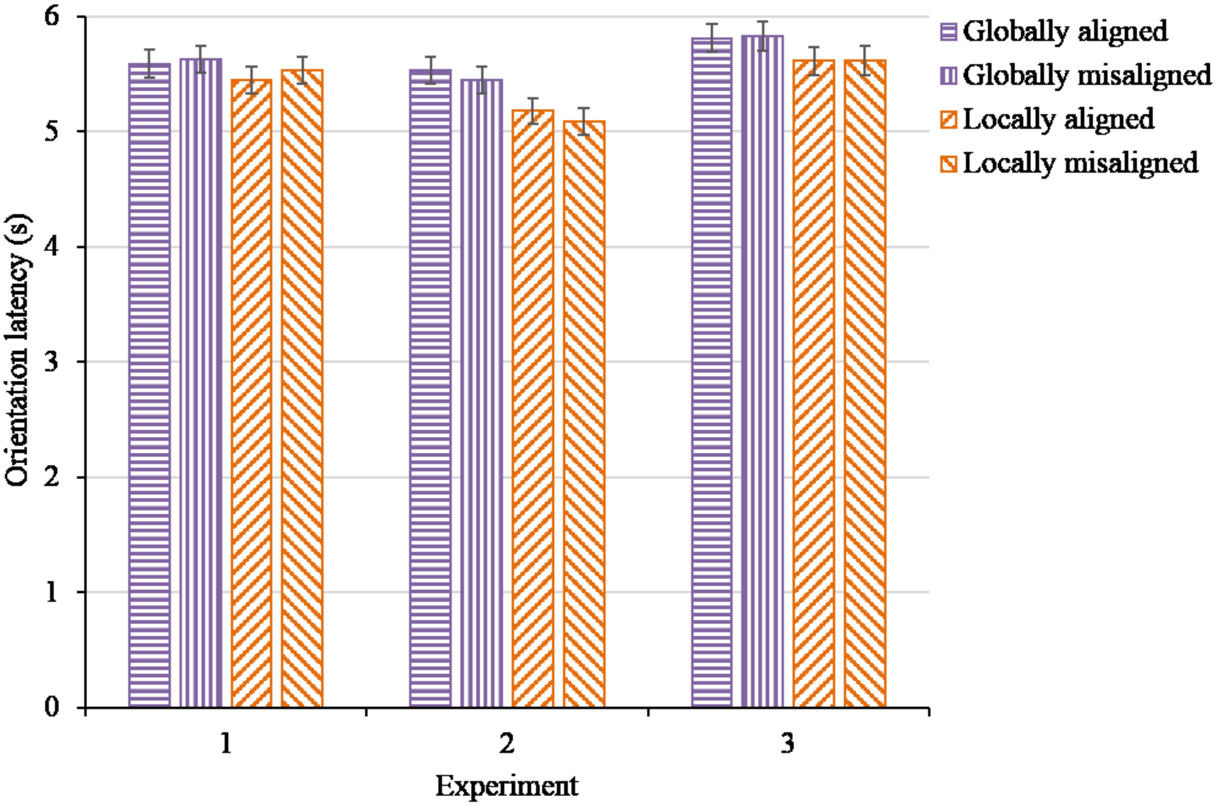

Figure S3.1. The mean orientation latency for each trial type in all experiments. Error bars represent ±1 SE removing the variance from individual differences.

3.8.1.1 Experiment 1

The orientation latencies in the globally aligned condition and the globally misaligned conditions were not significantly different, $t(31) = 0.20$, $p = .846$, Cohen's $d = 0.05$, $BF_{01}= 7.16$, indicating a null global sensorimotor alignment effect.

The orientation latencies in the locally aligned condition and the locally misaligned conditions were not significantly different, $t(31) = 0.48$, $p = .637$, Cohen's $d = 0.12$, $BF_{01} = 6.53$, indicating a null local sensorimotor alignment effect.

3.8.1.2 Experiment 2

The orientation latencies in the globally aligned condition and the globally misaligned conditions were not significantly different, $t(31) = 0.69$, $p = .494$, Cohen's $d = 0.17$, $BF_{01} = 5.79$, indicating a null global sensorimotor alignment effect.

The orientation latencies in the locally aligned condition and the locally misaligned conditions were not significantly different, $t(31) = 0.57$, $p = .570$, Cohen's $d = 0.14$, $BF_{01} = 6.22$, indicating a null local sensorimotor alignment effect.

3.8.1.3 Experiment 3

The orientation latencies in the globally aligned condition and the globally misaligned conditions were not significantly different, $t(31) = 0.10$, $p = .920$, Cohen's $d = 0.03$, $BF_{01} = 7.26$, indicating a null global sensorimotor alignment effect.

The orientation latencies in the locally aligned condition and the locally misaligned conditions were not significantly different, $t(31) = 0.02$, $p = .988$, Cohen's $d < 0.01$, $BF_{01} = 7.30$, indicating a null local sensorimotor alignment effect.

3.8.2 Results of relative heading judgment

3.8.2.1 Relative heading judgment in Experiment 2

Figure S3.2A plots the response directions in the relative heading judgment task in Experiment 2. The correct allocentric response direction was 90° (i.e., standing at object 9 and facing object 7 in Figure 3.1). The circular mean of the allocentric response directions from all the participants was 131.02°, and the 95% confidence interval was [105.37°, 156.69°], which did not cover the correct direction of 90°. Instead, the responses were biased toward 180°, which was the direction if the participants relied on local structures to respond. These results indicate that the participants did not respond accurately according to the global relations between the learning and testing rooms, but rather they tended to respond based on the local structural similarity between the rooms.

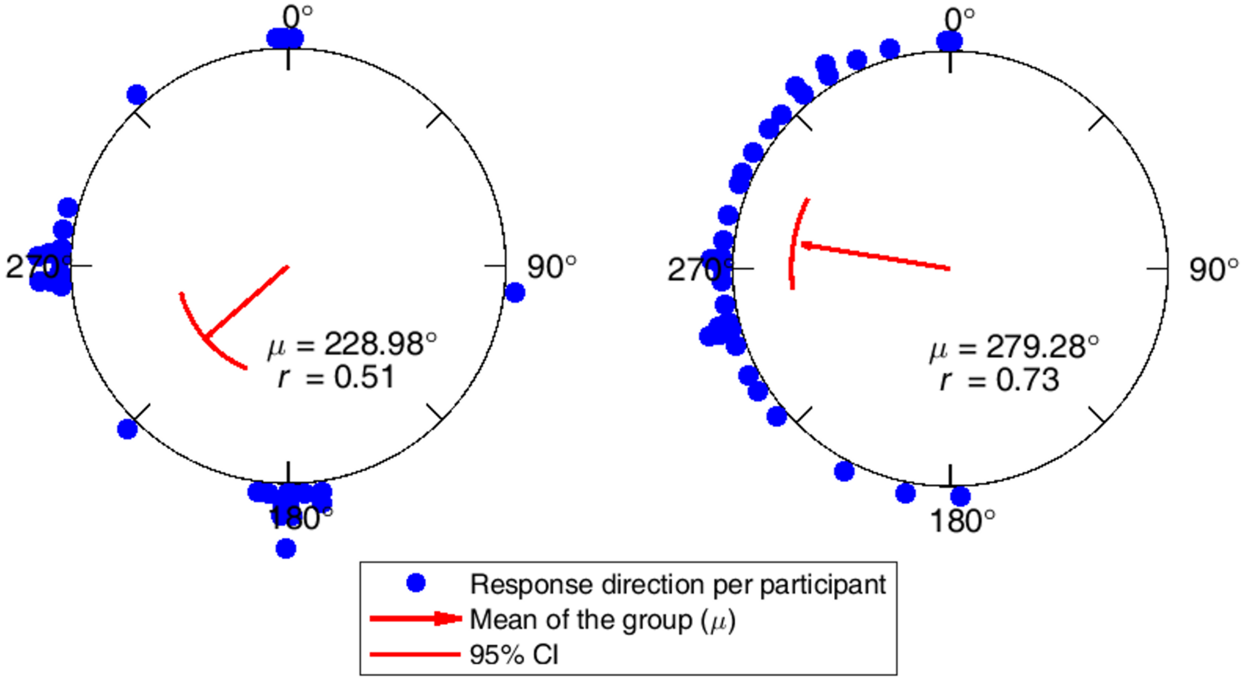

Figure S3.2. Response heading directions in the relative heading judgment task of Experiment 2 (A) and Experiment 3 (B). The correct heading direction is 90°. Each dot indicates the response direction from one participant. The red arrow shows the circular direction (μ) and the length (r) of the mean vector across all the participants. The red arc indicates the 95% confidence interval of the mean direction.

3.8.2.2 Relative heading judgment in Experiment 3

Figure S3.2B plots the response directions in the relative heading judgment in Experiment 3. The correct response direction was 90°. The circular mean of the response directions across all the participants was 80.72° and the 95% confidence interval was [65.11°, 96.34°], which covered the correct direction of 90°. These results indicate that the participants responded accurately according to the global relations between the learning and testing rooms. In addition, we conducted a Watson-Williams F-test (Mardia & Jupp, 2000, p.129) to test whether the response directions differed between Experiments 2 and 3. The result showed that the mean response directions in Experiments 2 and 3 were significantly different, $F(1, 62) = 11.43$, $p = .001$, suggesting that the responses in the relative heading judgment were better in Experiment 3 than in Experiment 2. The participants in Experiment 3 relied on the global representations of the learning and testing rooms to judge headings in the two rooms when there was no interference from local structural similarity.

Chapter 4 General Discussion

Humans often navigate in multiscale environments that contain several local spaces separated by boundaries. Through spatial navigation, navigators can update their self-location and develop spatial memory. Previous studies have shown that by extensive across-boundary navigation in multiscale environments, it seems effortless to develop local representations and update self-location relative to local boundaries or local features; however, it is difficult and requires preconditions to develop global representations and update self-location relative to global relations between locations across local spaces (Lei, Zhang, & Mou, 2020; Lei & Mou, under review; Marchette, Ryan, & Epstein, 2017; Marchette, Vass, Ryan, & Epstein, 2014; Spiers, Hayman, Jovalekic, Marozzi, & Jeffery, 2015; Wang & Brockmole, 2003). The current dissertation is aimed to investigate the function of one-shot across-boundary navigation in updating global self-location and developing global representations in multiscale environments. In Chapter 4, the findings in the two studies of Chapters 2 and 3 are summarized and then the implications by these findings are discussed.

4.1 Summaries

The study in Chapter 2 examined how people update self-location relative to global relations after one-shot across-boundary walking in a novel multiscale environment. The participants learned objects' locations at the learning location and then the blindfolded participants were led to physically walk to the testing location to conduct the JRD task. Experiment 1 manipulated the walking between the learning and testing locations to be either within a square room or between two visually different square rooms. The results showed comparable global sensorimotor alignment effects in groups of within- and across-boundary walking, indicating no effect of boundaries in updating self-location globally. The following experiments focused on one-shot across-boundary walking and tested the roles of some factors related to encoding and retrieval of global relations.

Regarding the encoding of global relations, Experiments 2 and 3 respectively removed the instructions for attention during walking (i.e., the instructions to pay attention to walking and keep track of the objects) and removed visual navigational affordance to another space (i.e., the door of the learning room). Regarding the retrieval of global relations, Experiments 4-6 focused on the JRD task and tested whether some factors of task trials that potentially increased the likelihood of using the original self-localization representations in long-term memory would affect the use of global representations. Experiment 4 tested two groups of the participants who did the JRD task with the imagined perspectives either including or excluding the learning orientation. Experiment 5 further included both the learning position and the learning orientation as the imagined viewpoint in the JRD trials. Experiment 6 intensified complexity of the imagined perspectives by increasing the number of the imagined perspectives in the JRD trials. All the manipulations in Experiments 2-6 did not influence the global sensorimotor alignment effects. Therefore, by one-shot across-boundary walking in a novel multiscale environment containing two local spaces, people develop global representations and update their self-location globally; moreover, the encoding and retrieval of global relations across boundaries seem automatic.

The study in Chapter 3 investigated the interference from the visual similarity of structures in local spaces on updating self-location globally. Similar to the study in Chapter 2, the participants still learned objects in one room and then had one-shot across-boundary walking into a novel room for testing. The main difference was that the two rooms in the study of Chapter 3 were rectangular rooms that were globally misaligned (i.e., the longest axis of one room was oriented north-south while the other one was east-west). The two rooms, which shared similar structures but globally misaligned, made it possible to differentiate local and global relations between the rooms. Updating self-location between the two rooms could occur by *visual re-anchoring* that leads to local sensorimotor alignment effects, or *global-path-integration* that leads to global sensorimotor alignment effects. The independent hypothesis stipulated that *global-path-integration* functions independently of *visual re-anchoring*, whereas the interference hypothesis stated that *visual re-anchoring* interferes with *global-path-integration*.

In Chapter 3, Experiment 1 had the participants walk one-shot between the two misaligned rectangular rooms and the results showed only local but no global sensorimotor alignment effects. Inspired by previous studies (e.g., Burte & Hegarty, 2004), Experiments 2 and 3 activated global representations by judging relative headings between the rooms, prior to the JRD task. The participants in Experiment 2 did the relative heading judgment while seeing the testing room, and the results still showed only local but no global sensorimotor alignment effects. In Experiment 3, the testing room was not visually presented until the participants finished the relative heading judgment, and the results showed both local and global sensorimotor alignment effects. These results indicate that after one-shot walking between two local spaces that are structurally similar but globally misaligned, *visual re-anchoring* interferes with *global-path-integration*, supporting the interference hypothesis. This interference occurs during activating global representations onto the sensorimotor level. After successful activation of global representations, people can update their self-location globally and develop global representations.

4.2 Implications of current findings

The studies in the current dissertation provided insight into the function of across-boundary navigation in developing global representations in multiscale spaces and the reason for the difficulty in this process. In this section, I will discuss four aspects of the implications of the current findings.

4.2.1 Function of path integration in global self-localization

Some researchers have claimed the important role of path integration in developing global representations of large-scale environments (Gallistel & Matzel, 2013; Jacobs & Schenk, 2003; Loomis et al., 1999; Milford & Wyeth, 2008), yet, empirical findings have challenged the contribution from path integration due to the difficulty in developing global representations after extensive navigational experiences in multiscale environments (Lei & Mou, under review; Lei et al., 2020; Marchette, et al., 2017; Marchette et al., 2014; Spiers et al., 2015; Wang & Brockmole, 2003). The robust global sensorimotor alignment effects in six experiments of Chapter 2 have provided evidence that after one-shot across-boundary walking between two local spaces, updating self-location by *global-path-integration* functions smoothly. Encoding global relations by path integration seems automatic and is not affected by the existence of boundaries. Retrieving global representations developed by path integration as sensorimotor representations seems automatic as well. Therefore, the error-prone nature of path integration (Etienne & Jeffery, 2004; Souman, Frissen, Sreenivasa, & Ernst, 2009; Zhao & Warren, 2015) or the existence of boundaries (McNamara, 1986; Radvansky & Copeland, 2006; Spiers et al., 2015) did not affect the function of path integration to develop global representations of two local spaces.

However, the global representations developed by path integration based on one-shot across boundary walking may be primitive and may be neither well-integrated nor enduring. By contrast, the global representations developed by path integration based on extensive across-boundary navigation and prior global learning (Lei & Mou, under review; Lei et al., 2020) may be more integrated and more enduring. The difference in the fidelity of global representations can be reflected in the activation of global representations between the current dissertation and Lei and Mou (under review). In Experiments 2 and 3 of Chapter 3, the global representations could not be successfully activated unless the structurally similar testing room was visually presented after relative heading judgments were finished. In Lei and Mou (under review), the global representations could be activated when the participants saw the structurally similar testing room before relative heading judgments. The global representations developed by one-shot across-boundary walking might be disrupted more easily by visual structural similarity than those developed by extensive across-boundary navigation and prior global learning. Thus, although path integration seems to function automatically to update global self-location and develop global representations across boundaries, the resulting global representations may not be well-developed and enduring.

Furthermore, as discussed in Chapter 2, it is not clear whether the findings of updating self-location by *global-path-integration* can be generalized to complex walking paths and complex multiscale environments which contain more than two local spaces. The noisy nature of path integration, coupled with the limited capacity of working memory (Baddeley, 2003), may not be able to accurately keep track of spatial relations along complex walking paths and in multiscale environments with plenty of local spaces. In addition, the studies in Chapters 2 and 3 enabled the participants to execute full-body movement in one-shot across-boundary navigation rather than visual movement only (Marchette, et al., 2017; Marchette et al., 2014) or partial body movement such as physical rotation with visual translation (Lei & Mou, under review; Lei et al., 2020), which might facilitate the function of path integration (Chance, Gaunet, Beall, & Loomis, 1998; Ruddle, Volkova, & Bülthoff, 2011). When people are in lack of full body-based cues in path integration, the requirements for extensive navigational experience (Carpenter, Manson, Jeffery, Burgess & Barry, 2015; Han & Becker, 2014) and some prior global learning (Lei & Mou, under review; Lei et al., 2020) may still be needed to develop global representations in multiscale environments.

4.2.2 Interference from piloting on path integration in global self-localization

The study in Chapter 3 showed that when the structural similarity between the learning and testing rooms, in addition to path integration during across-boundary walking, could also determine self-location in the testing room relative to the learning room, the robust global sensorimotor alignment effects shown in Chapter 2 disappeared. The study in Chapter 2 did not enable *visual re-anchoring* in self-localization since the shape of the square with the same wall colours could not decisively determine self-location locally. When the updated self-location by *visual re-anchoring* conflicted with that by *global-path-integration*, there was no evidence for global self-localization. As shown in Experiment 1 of Chapter 3, the participants relied on visual cues of local structures to update their self-location relative to the learning room instead of using global relations by path integration, although the learning procedure and the walking path were the same as in the study of Chapter 2.

This strong overshadowing effect from piloting (visual cues) on path integration (self-motion cues) is consistent with some previous findings in neurological studies. As mentioned in Chapter 1, place cells and grid cells of rats exhibit spatial field repetition when foraging in a multiscale environment with several visually similar compartments (Derdikman et al., 2009; Spiers et al., 2015). When the rats moved to a new track/compartment that was visually the same as the previous one, the visual cues of the local boundaries or local features could reset path integrator such that place cells and grid cells would repeat firing fields spatially similar to other tracks/compartments. Thus, in Experiment 1 of Chapter 3, after the participants walked to and visually saw the novel testing room, the participants used visual cues to update their headings locally and reset path integration to support their navigation (e.g., physical turning) in the testing room.

Moreover, the current findings shed light on the relationship between visual cues and self-motion cues. Previous studies have shown cue interaction between visual and self-motion cues in self-localization and homing. Cue combination (e.g., Bayesian cue combination to achieve optimal estimates, Ernst & Banks, 2002) of visual and self-motion cues can occur when both of them are available and valid. Visual cues are more reliable and are assigned higher weights compared with self-motion cues (Sjolund, Kelly, McNamara, 2017; Zhang, Mou, Lei, & Du, 2019). Cue competition (e.g., relying on one cue and ignoring the other cue, Chen, McNamara, Kelly, & Wolbers, 2017) can also occur when there is a discrepancy in estimation by visual cues and self-motion cues. Visual cues can correct and reset path integration (e.g., Tcheang, Bülthoff, & Burgess, 2011; Whishaw & Brooks, 1999), and path integration can be a backup system to detect large shifts of landmarks (Zhao & Warren, 2015). In contrast to cue interaction, the current dissertation shows the independence of piloting and path integration and that the estimates from visual and self-motion cues can coexist. As shown in Experiment 3 of Chapter 3, there was a coexistence of the updated self-location determined by visual cues and that determined by self-motion cues. The cues that target on different environmental scales do not interact and independently determine self-location in multiscale environments.

4.2.3 Spatial navigation and global self-localization

In a novel multiscale environment, spatial navigation simultaneously updates navigator's self-location and develops spatial representations of the environment. This applies to humans (Etienne & Jeffery, 2004; Foo, Warren, Duchon, & Tarr, 2005), non-human animals (Collett,

Collett, & Wehner, 1999; Wehner and Müller, 2006) as well as robotics (Milford & Wyeth, 2008, 2010). The current dissertation, to some extent, uncovers the processes of how navigation localizes navigators and develops spatial memory in different environmental scales.

After one-shot across-boundary walking between two square rooms, the participants could potentially reply on two kinds of spatial representations to conduct the JRD task. One is the original representations of objects from the learning orientation in long-term memory, which are irrelevant to the current self-location. The other one is the updated representations of the objects from the current self-location in working memory. In the study of Chapter 2, during across-boundary walking to the testing location, the updated representations were generated based on global relations between self-location and the objects' locations in the learning room; after the participants arrived at and visually saw the testing room, the square shape with four identical walls could not localize them relative to the learning room, and the primitive global representations remained actively rehearsed by cognitive efforts and might become more integrated and enduring. Thus, the participants primarily used updated global representations as sensorimotor representations and showed global sensorimotor alignment effects. In this process, spatial navigation updates global self-location and develops global spatial memory smoothly without any difficulty.

By contrast, in the study of Chapter 3, in addition to the original representations of objects from the learning orientation in long-term memory, the updated representations of the objects from the current self-location could be based on both local and global relations between misaligned rectangular rooms. During across-boundary walking to the testing room, the updated representations were still based on global relations between self-location and the objects; however, when the participants visually saw the testing room, the rectangular shape with a window on one short wall localized them relative to the learning room based on the local structures. The rehearsal of primitive global representations might be disrupted. Since the local representations were supported by visual cues whereas the primitive global representations were supported by cognitive efforts, the local representations were easier to maintain whereas the primitive global representations were in idle and might fade away without rehearsal. Thus, the participants used the updated representations, which were local, as sensorimotor representations in the JRD task.

To save the primitive global representations from disruption, they had to be actively maintained and rehearsed by cognitive efforts to attend to global relations. One trial of relative heading judgment that requires the retrieval of global relations between local spaces was used. Because the visual cues of local structures blocked the activation and retrieval of global relations, the activation of the global representations could succeed only when the visual cues of similar local structures did not exist prior to and during the relative heading judgment. After the global representations were activated and retrieved, the updated representations based on global relations remained actively rehearsed and might become enduring global representations. The existence of visual structural similarity did not interfere with the use of global representations after activation. The participants then used two kinds of sensorimotor representations, based on the locally and globally updated representations, to perform the JRD task.

The difficulty in developing global representations in multiscale environments reported in the previous studies (Lei & Mou, under review; Lei et al., 2020; Marchette et al., 2017; Marchette et al., 2014; Wang & Brockmole, 2003) may be due to the disrupted process in developing enduring global representations (which may be more integrated and stored in long-term memory) from primitive global representations (which may be more piecewise and stored in working memory). To solve this difficulty, one possible way is to remove disrupting factors. These disrupting factors could be the visual similarity of local structures as shown in the study of Chapter 3, and could also be other processes that occupy high cognitive loads such as complex math calculations (Konstantinou, Beal, King, & Lavie, 2014) or occupy visuospatial sketchpad in working memory by some other spatial-related tasks (Awh, Jonides, & Reuter-Lorenz, 1998). The other possible way is to enhance the fidelity of the global representations developed by path integration so that the global representations are more immune to disruption. This is where rich self-motion cues in across-boundary navigation (Ruddle et al., 2011), extensive navigational experience (Starrett, Stokes, Huffman, Ferrer, & Ekstrom, 2019), prior global learning to scaffold subsequent new spatial knowledge (Lei & Mou, under review; Lei et al., 2020), explicit instructions to attend to global relations (Shine, Valdés-Herrera, Hegarty, & Wolbers, 2016), and tasks requiring the use of global relations (Burte & Hegarty, 2004; Sholl, Kenny, & DellaPorta, 2006), may play important roles to facilitate the integration of global relations across local spaces and the development of enduring global representations.

4.2.4 Multiscale self-localization and spatial memory

Coexistence of local and global self-localization and spatial memory in multiscale environments shown in the current dissertation have also been demonstrated in the previous studies (Lei & Mou, under review; Lei et al., 2020). However, the exact neurological basis for multiscale spatial representations is not clear. Spatial representations in local and global scales are evident in rodent neurophysiological and human neuroscientific studies. Previous studies testing rats in a large environment without across-boundary foraging have shown that grid cells, place cells, and head direction cells may accommodate with different spatial scales. Grid cells of rats can encode spatial metric in multiple scales of an enclosure (Hafting et al., 2005).

Recordings made on rats in very large spaces suggested that some place fields can span the entire length of an eighteen-metre track (Kjelstrup et al., 2008). Some head direction cells of rats could show bi-directional tuning to local environmental cues and global directions (Jacob et al., 2017). In addition, the longitudinal axis of the hippocampus which contains place cells, supports a gradient of representation scales in rodents (Strange, Witter, Lein, & Moser, 2014) and humans (Brunec et al., 2018), with ventral-to-dorsal/anterior-to-posterior gradient of coarse-to-fine spatial representations.

Although these findings are based on navigation in large-scale environments with no boundary-crossing, the representation for multiple scales by the characteristics of spatial cells as well as hippocampal longitudinal axis may still apply to across-boundary navigation in multiscale environments. The fine-grained local spatial relations developed by piloting may be represented by smaller sizes of place and grid firing fields with fewer overlaps between the firing fields, and the coarse global spatial relations across boundaries developed by path integration may be represented by larger sizes of place and grid firing fields with more overlaps between the firing fields. Head direction cells may exhibit bi-directional tuning to local directions determined by local environmental cues and also to global directions based on spatial relations across boundaries. Similarly, the ventral/anterior hippocampus may encode global spatial relations across boundaries and the dorsal/posterior hippocampus may encode local spatial relations.

Moreover, neuroimaging studies on human participants in multiscale environments that contain several local spaces showed that the retrosplenial complex may be responsible for both local and global directional coding. In Marchette et al. (2014), the participants learned an environment with four geometrically similar museums in desktop virtual reality and developed local but no global representations. The activity patterns in the retrosplenial complex were similar for the same local directions or local positions across museums, irrespective of global directions or global positions, demonstrating that the retrosplenial complex could represent local directions and positions. Shine and colleagues (2016) also tested participants in an environment with four local rooms but in an immersive virtual reality that allowed physical rotation. The participants in their study were explicitly instructed to encode global directions of views inside local rooms, and they developed global heading representations. Retrosplenial cortex and thalamus, both containing head direction cells (Taube, 2007), were activated when the participants were shown pictures of local views and judged global orientations. Thus, the human retrosplenial complex may be responsible to encode multiscale heading representations by navigation in multiscale environments. Future studies may be needed to test these insights and reveal the neural basis for multiscale spatial representations of across-boundary environments.

4.3 Limitations and future research

The current studies have some limitations that may be addressed in future studies. First, the current studies enabled full self-motion cues in path integration during across-boundary navigation, but it is not clear which component of path integration is important. By one-shot across-boundary walking, the study in Chapter 2 found robust global self-localization in all six experiments and the study in Chapter 3 showed global self-localization when the global representations were activated. Although it is clear that path integration functions across boundaries to develop global spatial representations by one-shot walking, it remains unclear which component of path integration (optic flow and body-based cues such as proprioceptive information, vestibular information and motor efference copy) is critical in this process. For example, some studies have shown that people can rely on optic flow to estimate objects' locations (Waller, Loomis, & Steck, 2003) whereas other studies have shown that optic flow is not sufficient to update people's positions in navigation (Ruddle & Lessels, 2009). The full-body movement used in the current studies can be replaced by partial self-motion (e.g., optic flow alone by using a joystick to move visually, or vestibular information alone by being wheeled while blindfolded) to examine the contribution from specific components of path integration to develop global spatial memory in multiscale environments.

Second, the current studies were based on across-boundary walking that occurred only once. Especially in the study of Chapter 3, the strong interference from the local structural similarity in activation of the global representations may be reconciled by factors such as multiple times of across-boundary walking and some prior global learning of the environment (Lei & Mou, under review; Lei et al., 2020). Future studies may further explore critical conditions that lead to automatic global self-localization between structurally similar local spaces without the need to activate the global representations.

Third, the multiscale environments used in the current studies were simplified and lack of environmental complexity as in real life. One issue is that the multiscale environments in the current studies only contained two rooms with a relatively simple path linking them. However, real-life environments are often much more complex. For example, a campus building may contain plenty of offices/classrooms with different sizes but similar layouts, and there may be many possible routes connecting different offices/classrooms that have various path lengths and turning angles. It remains unknown that to what extent of environmental complexity, path integration can update self-location globally and develop global representations. The other issue is that the boundaries of local rooms in the current studies completely blocked visual cues outside and the participants were only able to perceive visual cues of the immediate space. Yet, in daily life, there are usually windows in local spaces and hallways that permit visual cues from the global environment outside. These distal cues may play an important role to facilitate path integration in global self-localization, especially when the multiscale environment is complex with plenty of local spaces and complicated walking paths connecting them. Future study may examine the influence of complex walking paths, an increased number of local spaces and the existence of distal landmarks in developing global spatial memory.

Finally, so far it is not clear how human and non-human brains encode headings, positions, and distances in local and global scales of an environment with across-boundary spaces. Neuroscientific studies, such as single-unit recordings on rodents and neuroimaging studies on humans, may be required to investigate this question.

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