From horizontal to vertical: Human spatial representations in three-dimensional navigation

by

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Abstract

Previous research has provided a lot of evidence about spatial navigation on 2D surfaces whereas how animals represent space in 3D navigation involving vertical information is much less often investigated (Jeffery, Jovalekic, Verriotis, & Hayman, 2013; Jeffery, Wilson, Casali, & Hayman, 2015). The current dissertation work aims to investigate humans' memory of localization and their heading updating in 3D navigation. In Chapter 1, I first review the previous research about these two topics (3D location memory and 3D heading) and briefly discuss the individual difference by evolutionary and individual histories. Chapter 2 presents Study 1 which examined 3D location memory and Chapter 3 presents Study 2 which examined 3D heading representation in spatial navigation. Both studies were conducted in immersive virtual reality environments. Chapter 4 summarizes the findings in the two studies and discusses the general cognitive mechanisms and principles in 3D navigation implied by the two studies.

Study 1 presented in Chapter 2 investigated whether humans' localization is more variable vertically than horizontally in different locomotion modes. Participants localized targets on a vertical wall via self-locomotion. One group of participants flew three-dimensionally along their viewing direction towards the target (flying group). The second group only locomoted on the floor and the wall along the projection of the viewing direction onto the current travelling surface (climbing group). The third group pressed a button to be teleported from the floor to the wall and then locomoted on the wall (teleportation group). Both the flying and the climbing groups showed a horizontal advantage of location memory whereas the teleportation group showed a vertical advantage. Examining the trajectories of the participants in the three groups indicate a vertical advantage of locomotion on a vertical surface. The results suggest that locomotion mode does not account for the horizontal advantage for the surface-travelling animals. Therefore, the horizontal advantage is more likely to be species-specific rather than locomotion-mode specific.

Study 2 in Chapter 3 investigated whether humans can spontaneously extend their allocentric heading on the ground when locomoting to walls and the ceiling. Participants first learned a layout of objects on the ground. In testing phases, initially facing south (or north), they navigated to testing planes: south (or north) walls with the testing heading of Up or the ceiling with the testing heading of North (or South). They then either replaced the objects on that plane or did a Judgement of Relative Direction task (JRD task, “imagine standing at object A, facing B, point to C”) with imagined headings of south and north. The results from the object placement task showed that the participants more likely treated Up on two opposite walls, and the same direction (e.g., North) on the ceiling and on the ground as the same heading. Only a small portion of participants (about 20%) treated the same directions on the ground and on the ceiling as two opposite headings, indicating that they extended their allocentric heading through pitch rotations. The results of the JRD task showed that only these “extension” participants showed a reversed sensorimotor alignment effect, better performance when the imagined facing direction on the ground and physical facing direction on the ceiling were opposite than when they were the same. These results indicate that on a behavioral level, only a small portion of humans can spontaneously represent 3D allocentric headings (i.e., pitch) while most humans only represent 3D allocentric directions (e.g., North, Up). Therefore, the toroidal (extension) model proposed by findings in bats and rats (Finkelstein et al., 2015; Page et al., 2018; Taube et al., 2013) may not be applicable to humans.

Supplemental material related to this thesis is available at https://era.library.ualberta.ca/collections/7p88ck40x.

Preface

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Chapter 1 Introduction

All mobile organisms live in a three-dimensional world. In natural environments, there are terrains with slopes, hills and mountains. In artefactual environments, there are walls, multi-floor buildings and towers. These 3D features are useful to navigate in the environments. Successful navigation in such a three-dimensional world is essential to the living of all mobile organisms. Animals forage food and look for shelters in natural environments. Humans commute from home to work and move around in the city. Therefore, both humans and non-human animals need to remember the important locations to them (e.g., home) and know how to get to those places by navigation. It is fundamental and adaptive to have the abilities of a) localizing goal objects and b) establishing orientation in the environment[1]. For example, a bird need to know that its nest is on the tree which is north of the river and two meters away from the building in order to return to it. It has to localize the nest by environmental cues such as landmarks and environmental geometry and also determine its heading (i.e., which is north) when it flies across the river to the nest.

For humans, it seems natural to divide the world into two sections—the ground we stand on (horizontal dimensions) and the sky or underground space most of us can rarely reach (vertical dimension). In this dissertation work, the “horizontal” dimension is defined as the dimension that is perpendicular to gravity whereas the “vertical” dimension is defined as the dimension that is parallel to gravity. In other words, the horizontal and vertical dimensions are not relative to the observer’s perspective but to the gravity.

Every mobile human has experience of navigating on horizontal planes, at least in artefactual environments, while most humans have rare experience navigating vertically unless in some artefactual environments (e.g., taking an elevator or rock climbing). Previous studies have

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[1] In this dissertation work, the word “environment” is referring to navigable space on the earth, including artefactual enclosures, rooms and natural environments, and will not be distinguished from each other.

shown that in either section (horizontal and vertical), there are a variety of cues that can help us to navigate. For example, on horizontal surfaces, the geometric shape of a navigable environment with continuous surfaces is a salient orienting cue (for review, see Cheng, Huttenlocher, & Newcombe, 2013; Cheng & Newcombe, 2005). Human children can use the geometric shape of the environment to orient from a very young age (Hermer & Spelke, 1996, 1994). In vertical dimension, for example, wall height can be used by 4-year-old children to orient (Hu, Zhang, Wu, & Shao, 2015).

Navigating in this 3D world can be very complicated. For clarification, in this dissertation work, 2D navigation refers to physical movements along a 2D horizontal plane. 3D navigation not only refers to the movements across interconnected planes (multilayered navigation) or unconstrained movements through 3D space (volumetric navigation) as defined by previous researchers (Finkelstein, Las, & Ulanovsky, 2016) but also includes movements on vertical surfaces. For example, locomoting on a horizontal floor would be 2D navigation according to these definitions, but first locomoting on the floor and then climbing up along the vertical wall would be 3D navigation.

Previous research has provided numerous evidence for spatial abilities on 2D surfaces whereas the question of how humans use information from the vertical dimension in navigation is much less often investigated than the question about information from horizontal dimensions (Hu et al., 2015; Jeffery, Jovalekic, Verriotis, & Hayman, 2013; Jeffery, Wilson, Casali, & Hayman, 2015). From the evolutionary view, the vertical cues beyond a Euclidean plane should not be ignored. In natural settings, terrain features such as a mountain's height or the slope of the ground can provide stable, reliable information which presumably could guide three-dimensional navigation for mobile organisms. In ancient times, humans may have spent much more time navigating three-dimensionally for survival (e.g., climbing on the trees to forage). Jeffery et al. (2013) proposed that the vertical axis, once determined, can be used as a reference frame for the encoding of metric information for both direction and distance. For example, one can use body head-foot vertical axis as well as horizontal axes (left-right, front-back) to establish an egocentric reference frame. Note that in this dissertation work, vertical cues refer to the cues that could be used in guiding 2D or 3D navigation. Using a remote mountain to find north on the horizontal ground would be an example of using vertical cues in 2D navigation. Using the changes of one's body head-foot vertical axis to find one's heading would be an example of using vertical cues in 3D navigation. Furthermore, the same cue may be used in different ways. For example, a remote mountain can served as a landmark indicating the direction north for 2D navigation whereas a rock climber on a steep slope of this mountain can use the steepness to track his or her own location. The mountain serves as a pure visual cue in the former case but presents both visual and idiothetic information in the latter case.

The current dissertation work aims to investigate humans' memory of localization and their heading updating in 3D navigation. In Chapter 1, I first review the previous research about these two topics (3D location memory and 3D heading) and briefly discuss the individual difference by evolutionary and individual histories. Chapter 2 presents Study 1 which examined 3D location memory and Chapter 3 presents Study 2 which examined 3D heading representation in spatial navigation. Chapter 4 summarizes the findings in the two studies and discusses the general cognitive mechanisms and principles in 3D navigation implied by the two studies.

1.1 Three-dimensional localization in navigation

Localizing a target object is common in humans' life. For example, to find a specific office within a building, you have to know which level of the office is on. If each floor of the building contains a lot of offices, to locate it accurately, you have to know the office's location relative to the edges of the floor (e.g., close to the corner) or relative to some landmarks (e.g., next to the elevator). Humans spend most time on the horizontal surface (ground) but occasionally they also navigate on vertical surfaces in activities like rock climbing or locomote in both horizontal and vertical directions like going up slopes or stairs. Furthermore, previous research indicates that people often get lost in buildings with bad designs, which is also related to people's spatial ability (Carlson, Hölscher, Shipley, & Dalton, 2010). Therefore, it is meaningful to examine the spatial memory of localizing targets with both horizontal and vertical components.

1.1.1 Behavioral evidence on 3D localization

For humans, processing vertical information seems more difficult than processing horizontal information. When humans learned two separate and overlapping routes on different floors in a building, they could integrate the relationship between the two routes. However, when asked to point to vertically aligned locations between the two routes, participants' responses were less accurate and slower than those when pointing to locations within one route (Montello & Pick, 1993).

With the help of virtual reality techniques, researchers have examined the encoding of vertical information in multi-level environments with more strict experimental control to exclude the potential influence of path integration system, which is a process of monitoring one's position in space from velocity or acceleration signals provided by inertial cues and optic flow (Etienne & Jeffery, 2004; Klatzky, Loomis, Beall, Chance, & Golledge, 1998).

When making distance judgements between locations across floors (e.g., standing on the second floor, point to objects on the first and third floors), human participants tend to make errors in upward and downward judgements. Furthermore, such errors seem to be asymmetrical: they made greater downward errors when making upward judgments than upward errors when making downward judgments (P. N. Wilson, Foreman, Stanton, & Duffy, 2004). A follow-up study showed similar results (Tlauka, Wilson, Adams, Souter, & Young, 2007). It seems that the vertical space is biased towards the horizontal dimension.

Thibault, Pasqualotto, Vidal, Droulez and Berthoz (2013) found the initial learning mode can influence humans' encoding in a multi-floored environment. In a virtual reality environment, participants navigated in the same building through either "planar" or "columnar" exploration. After the learning phase, particitpants re-experienced a segment of the exploratory route as a spatial memory test. The results showed that the group of participants who explored the building with planar routes had better spatial memory performance than the group with columnar routes. However, for both groups, the spatial memory task was better performed when participants re-experienced the routes with the same learning mode as during the learning phase. This suggests that three-dimensional environments could be explored and stored according to any fashion (i.e., planar or columnar), which seems to be determined by the initial learning mode, not absolute axes (i.e., horizontal or vertical). Recently, the effect of learning mode has been replicated in a cylindrical environment with multiple floors (Dollé, Droulez, Bennequin, Berthoz, & Thibault, 2015).

Some studies in other spatial tasks also indirectly indicate that humans encode vertical information differently from horizontal information for localization. Humans can accurately perceive objects' location on top of a vertical stick if the stick is within arm's length and not higher than a person's height (Giudice, Klatzky, Bennett, & Loomis, 2013). However, such results may not be true when the target location is farther away from the observer. In both outdoor and virtual environments, humans consistently overestimated height relative to egocentric distance (Higashiyama & Ueyama, 1988; Li, Phillips, & Durgin, 2011). One study showed that humans tend to underestimate the angle through which they move in the horizontal plane. However, either no bias or an overestimate of movement angle is found in the sagittal plane, which suggests that humans' path integration system operates differently in all three dimensions (Barnett-Cowan, Meilinger, Vidal, Teufel, & Bülthoff, 2012). Some previous studies on spatial language suggest that the vertical-horizontal distinction may be semantically, and perhaps conceptually, privileged, at least in English (K. J. Holmes & Wolff, 2013; Landau & Jackendoff, 1993).

The research reviewed above indicates that humans encode vertical information differently from horizontal information for localization but most of the studies used a multi-level building rather than a 3D volumetric space. When passively moved within a 3D space in both horizontal and vertical dimensions, humans showed similarly accurate memory for vertical and horizontal locations (Kim, Jeffery, & Maguire, 2017), which seems to be inconsistent with the findings in other studies. Note that this study presented visual stimuli to the participants and thus the participants only did passive movements. Furthermore, this study did not disassociate all three dimensions but let participants to move in combination of two or three dimensions.

Some animal research examined memories in a three-dimensional space and suggests that mammals may have a horizontal memory advantage when both horizontal and vertical information about the locations is required, especially in 3D volumetric navigation. For example, mice show larger errors in localization in a 3D maze than in a 2D horizontal maze (J. J. Wilson et al., 2015). But this study also used apparatuses which allowed the animals to move in combination of two or three dimensions (e.g., moving in both horizontal and vertical dimensions) thus should be seen as indirect evidence in addition to the place cell research shown in the following section.

1.1.2 Neural evidence on 3D localization

Some neuroscience research in non-human animals also suggests that the horizontal and the vertical information for a location may be encoded differently. Place cells in hippocampus, first discovered by O'Keefe and colleagues (O'Keefe & Dostrovsky, 1971), have been found to be more likely to be oriented by using a sloping surface than other cues in the environment (e.g., distal landmarks), suggesting that place cells are sensitive to changes in elevation to represent locations (Jeffery, Anand, & Anderson, 2006; Knierim & McNaughton, 2001). Place cells are also found to be sensitive to vertical displacement in circumstances like microgravity environment where vestibular information is unlikely available (e.g., in outer space) (Knierim, McNaughton, & Poe, 2000). Place cells of rats have a larger firing field vertically than horizontally when locomoting on a vertical pegboard (Hayman, Verriotis, Jovalekic, Fenton, & Jeffery, 2011). This suggests that rats may encode the vertical component of space with larger errors than the horizontal component.

Grid cells, as a source of distance information to place cells, are neurons that fire at multiple locations in an environment. Grid cells fire periodically on horizontal planes and the firing fields form a repeating hexagonal grid-like pattern which supply odometric (distance measuring) information. However, Hayman et al. (2011) suggest that grid cell odometry is impaired or absent in the vertical domain, at least when the rat itself remains horizontal locomoting on a vertical pegboard. By modeling on grid cells, researchers found that the firing patterns of grid cells is not fixed in absolute 3D space but is influenced both by the surface the animal is on and by the relationship of this surface to the horizontal (Hayman, Casali, Wilson, & Jeffery, 2015).

However, these neural studies did not provide testing conditions with changes purely in the vertical dimension. Instead, the tracks in these studies were actually relatively complex and across three dimensions, or the free-foraging task led to complicated running routes. Using simplified tracks (rectangular or circular), Knierim and Rao (2003) found that when the running track was relocated in the testing room with changes in elevation, place fields responded relative to the track, rather than the cardinal coordinates of the room.

Furthermore, experimental design should also take the natural body orientation of the animals in the actual locomotion into consideration. For example, in Hayman et al. (2011), when the rats were navigating in the apparatuses and the place and grid cells firing was being recorded, the rats were actually horizontally oriented. In other words, although the whole route had vertical components, the steps along the route were mostly horizontally, not purely vertically oriented. Therefore, the recorded data may not reflect the changes in firing fields during vertically-oriented locomotion but elevation in environment. If the rats had been vertically oriented, perhaps fields would have had a more typical, hexagonal pattern.

While single-neuron-recording animal research suggests that the vertical information may be encoded more variably than horizontal information, neuroimaging research in humans indicates different results on this question. An fMRI study in humans showed that right anterior hippocampus is sensitive to place changes along both horizontal and vertical axes (Kim et al., 2017). By contrast, other fMRI studies found that hippocampus is more engaged by horizontal than vertical motion (Indovina et al., 2013, 2016). But note that these studies only passively presented the visual motion information to participants, which may not fully reflect the ability in active navigation. Using positron emission tomography (PET), researchers found that there are two different pathways in the brain for processing horizontal and vertical navigation visual information about the environment (Zwergal et al., 2016). However, this study used a between-groups design that contrasted overall activation between two navigation conditions, which might be limitations to get a final answer to the question.

1.1.3 The purposes of Study 1

Based on previous evidence, a theory has been proposed. It states that spatial representation in three-dimensional world seems to be a set of 2D, planar encoding rather than a 3D, volumetric one (Jeffery et al., 2013, 2015). According to this theory, the horizontal advantage in spatial memory is caused by non-equal encoding mechanisms for spatial information in horizontal and vertical dimensions. The theory seems to be able to explain many findings in both behavioral and neural studies. However, this theory is based on mostly rodent evidence. Therefore, this model might not be equally appropriate for other species. For example, primates may have difference processing mechanisms compared to rodents. When macaque monkeys are merely looking from a distance at a particular spot, whose location has both horizontal and vertical components, the firing of hippocampal cells responds accordingly to the looking behavior (Georges-François, Rolls, & Robertson, 1999; Rolls, 1999).

Furthermore, horizontal advantage is not always found in all animals. For example, when bats fly through a volume, the firing fields of place neurons were not compressed or elongated in either dimension, unlike what was found in rats (Yartsev & Ulanovsky, 2013). In other words, for flying bats, the vertical and horizontal components of space appear to be encoded with equal errors. The findings in bats seem inconsistent with the planar-encoding theory (Jeffery et al., 2013, 2015) and suggest that not all the species have the horizontal advantage in memory. Bats navigate three-dimensionally very often (i.e., fly), thus might have evolved to have the cognitive mechanism adapted to such 3D navigation. They have spatial memory equally well in horizontal and vertical dimensions, which is possibly crucial for their survival.

The discrepancy about horizontal advantage findings could be species-specific and be relevant to evolutionary reasons, or be due to different locomotion modes of the animals used in previous studies (e.g., bats fly whereas rats do surface-based locomotion). Study 1 in this dissertation work (Chapter 2) aimed to differentiate the two possibilities. Humans' localization in horizontal and vertical dimensions was examined in flying and surface-based locomotion modes. The difference or similarity between the two groups would indicate whether the horizontal advantage is due to locomotion mode. Specifically, the targets were on a vertical wall therefore only the error in one horizontal dimension was compared with that in the vertical dimension. This also controls participants' movements when they moved towards the target on the vertical surface such that they could not change the position in two horizontal dimensions jointly.

The locomotion mode might affect localization, which may be due to difference preferences of animals for horizontal and vertical movements. For example, rats have a prioritization of horizontal over vertical movements on a vertical pegboard (Jovalekic et al., 2011), whereas non-surface-based animals do not have such preference (Flores-Abreu, Hurly, Ainge, & Healy, 2014; Holbrook & Burt de Perera, 2009). Although humans are surface-travelling animals, when making decisions on travelling route, they consider both the horizontal and vertical dimensions and try to avoid unnecessary efforts like climbing the hills (Layton, O'Connell, & Phillips, 2009). When navigating in a multi-level building, humans prefer to determine the vertical direction to the goal location (e.g., going up or down) before the horizontal one (Hölscher, Meilinger, Vrachliotis, Brösamle, & Knauff, 2006). It is not clear whether human participants had a prioritization of horizontal over vertical movements on a vertical plane towards a target. In addition, in Study 1, the participants started locomoting from the ground. When participants locomote on the ground before reaching the wall, they still can choose to locomote straight to the wall in the shortest distance or to locomote straight to the horizontal location of the target (i.e., the projection of the target location onto the floor). As a consequence, they still move both vertically and horizontally on the wall in the former whereas they only need to move vertically on the wall in the latter. Therefore, the second purpose of Study 1 is to examine which locomotion route is preferred by humans in surface-based locomotion that if they would choose the moving trajectory only on the wall or if they would choose the moving trajectory both on the ground and on the wall. Therefore, the trajectories of the surface-based locomotion group were recorded and analyzed.

1.2 Three-dimensional heading in navigation

For many mobile organisms, to obtain accurate directional heading is the first step in successful spatial navigation. To establish ones' orientation on the horizontal plane, individuals need to determine their body front relative to an allocentric reference direction on the horizontal plane (e.g., north). One's orientation (i.e., body front) relative to the allocentric reference system is termed as the allocentric heading (Klatzky, 1998). The ability to orient oneself on a horizontal plane has been examined in many studies across different species (for review, see Cheng, Huttenlocher, & Newcombe, 2013; Cheng & Newcombe, 2005). However, individuals navigate in a 3D environment (e.g., in a rectangular room with ceiling), which naturally has six allocentric reference directions (north-south, east-west, gravity up-down). Humans, as three-dimensional animals, naturally have three axes to the body: head/feet, front/back, or left/right (see Figure 1.1). Dynamic rotations relative to these axes can be defined as *yaw*, *roll*, and *pitch*, corresponding to rotations in the horizontal, coronal, and sagittal planes, respectively (Jeffery et al., 2013). The rotational transformation relation between ones' body axes (front-back, left-right, head-foot) and the allocentric reference directions (north-south, east-west, gravity up-down) will reflect ones' 3D allocentric headings. For example, when a rat locomotes from the ground to a vertical wall, it has to pitch 90°. Its facing direction on the wall would be *Up* which is not in the reference directions on the ground. To update its heading, the animal would have to perform mental pitch rotations to map *Up* back to the directions on the ground (e.g., North).

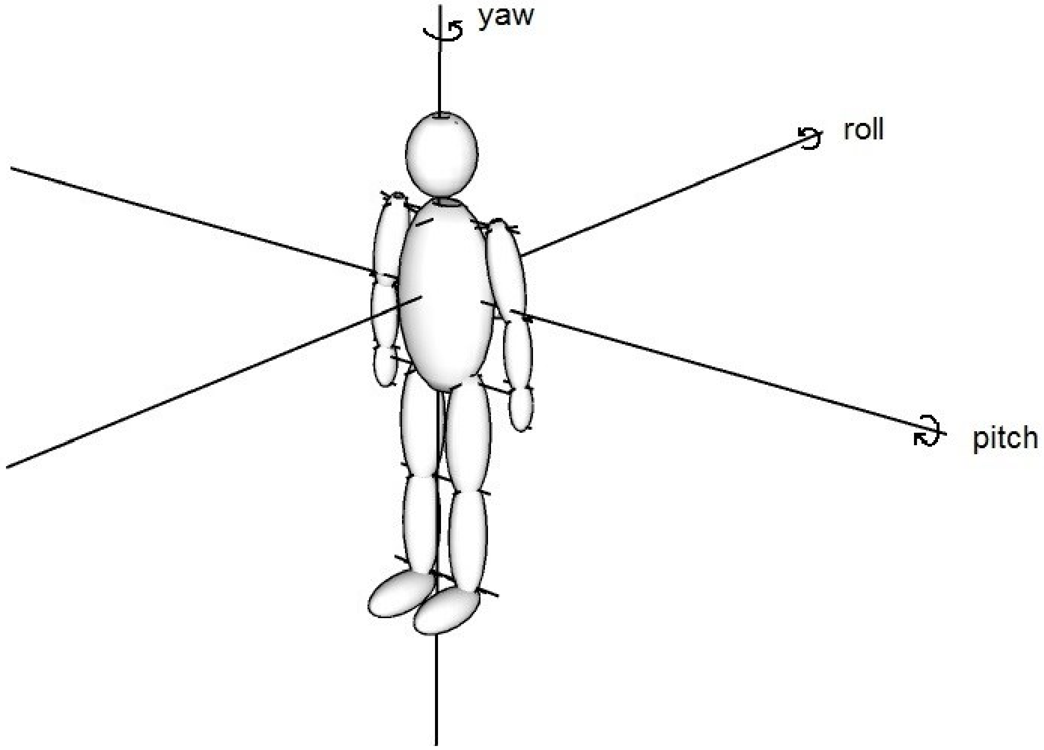

Figure 1.1. The three types of rotations (yaw, pitch, and roll) around human's body axes. The rotations are expressed in an egocentric reference frame (from the point of view of the individual).

Although there are many studies investigating how humans update allocentric headings on the horizontal plane (e.g., Waller, Montello, Richardson, & Hegarty, 2002), studies examining how humans represent and update their 3D allocentric headings are rare and mostly use animal neuron recording methods. Here I review some major neural studies examining this question.

1.2.1 Neural evidence on 3D heading representation

Directional information is encoded by head direction cells in brain, which fire as a function of the organism's heading in the horizontal (yaw) plane (Taube, 2007, 2011). Head direction cells have been found in a number of brain areas including anterior dorsal thalamic nucleus, lateral mammillary nuclei, retrosplenial cortex, and entorhinal cortex (for review, see Taube, 2007). Numerous previous studies have examined the firing of head direction cells in rodents when animals have different orientations on horizontal surfaces. For vertical information, certain head direction cell populations are sensitive for encoding of pitch and yaw in the lateral mammillary nucleus of the rats (Stackman & Taube, 1998). This finding suggests that at least some of the head direction cells can encode vertical directional information.

When an animal navigates on vertical surfaces (e.g., climbing up and down on a wall), head direction cells show interesting firing patterns, although such firing pattern may be influenced by a few factors. One study (Stackman, Tullman, & Taube, 2000) tested rats in a cylinder enclosure with a wire mesh ladder on one side of the inner wall and a horizontal annulus on top. No external cues were available. The rats were trained to retrieve food pellets from four positions on the annulus from bottom to the top by climbing the wire mesh during which the activity of head direction cells were recorded. Stackman et al. (2000) found that when the wire mesh was at the preferred firing direction of head direction cells during training, head direction cells fired at peak as the rats climbed up, but not as they climbed down. The firing direction was defined according to horizontal bottom surface. When the cylinder was rotated 180° relative to the preferred firing direction during training, cell firing maintained as the rats were climbing down, but not when climbing up. These results suggest that head direction cells can extend the horizontal coordinate system to vertical dimension in pitch 90°, but not in pitch 180°.

In a follow-up study (Calton & Taube, 2005), rats were trained in a three-dimensional box with four walls, a horizontal rectangular bottom and a horizontal ceiling to navigate from the bottom to the wall and then to the ceiling. Consistent with previous findings, when the rats were on vertical walls, head direction cells kept the same firing as when the rats were on the bottom, acting as if the vertical walls were extensions of the floor. For example, initially facing north wall on the bottom, when the rats navigated onto the north wall facing *Up*, the head direction cells kept the same firing pattern. Surprisingly, when the rats were at inverted positions on the ceiling, the signals of the head direction cells showed dramatic changes like disrupted by the change of the position and heading. These results further confirm that the signals from head direction cells do not follow the cardinal orientations in all 360°. A recent study showed that when rats move between vertical walls of different orientations, head direction cells rotate their activity by an amount corresponding to the amount of vertical-axis rotation, suggesting rotations of the local reference frame (J. J. Wilson, Page, & Jeffery, 2016).

Self-motion cues can affect the selection of reference frame for head direction cells (Taube, Wang, Kim, & Frohardt, 2013). Rats were trained on a horizontal board. The firing of head direction cells showed that in these horizontal sessions, they usually used the room as a reference frame rather than the board itself or local cues on the board. Later, the board was rotated to a vertical position and was placed close to the four walls of the testing room. When rats were moved passively from horizontal ground to the vertical board, head direction cells used the board cues, although room cues were available. This result suggests that the cells followed a local reference frame and maintained their preferred firing directions corresponding to the surface. In contrast, when the transition from a horizontal surface onto the vertical platform was in active movement, head direction cells remained the same firing patterns as if the walls were an extension of the floor, which indicates that the rats used the room as their reference frame. These findings highlight the important role that self-initiated locomotion cues play for maintaining and updating spatial orientation when moving in three dimensions.

The studies reviewed above only examined the movement of surface-travelling animals and their heads are mostly at the top or in front of the body. Recently, researchers found that bats, a mammal species that often invert their body upside down, represent heading in a 3D manner (Finkelstein et al., 2015; Rowland & Moser, 2015; Yartsev & Ulanovsky, 2013). When flying bats did pitch rotation movement in all 360°, such movement does not affect the head direction cells' firing patterns, which suggests that bats have a toroidal coordinate system therefore pitch rotation movement does not affect the azimuth head direction cells' firing patterns (Finkelstein et al., 2015). These findings suggest the possibility that animals may be more sensitive to cues in the dimensions in which they have more experience and that such evolutionary and ontogenetic experience may play a role in animals' navigation strategy. For example, bats perform pitch rotations a lot (e.g., pitch 180° to hang upside down on the ceiling of a cave) which is important for their survival. Therefore they might have evolved to adapt to this need.

Neuroimaging research in human participants found that the neural representations of the cardinal axes of motion (horizontal and vertical) are partially distinct, which suggests that yaw and pitch rotations might be processed in different mechanisms, at least in conditions that the motion information was visually presented (see Section 1.1.2) (Indovina et al., 2013, 2016). There might be a pure vertical encoding scheme in the right retrosplenial cortex and posterior hippocampus (Kim et al., 2017). Again, these studies only passively presented the visual motion information to participants, therefore may not directly answer the question whether humans have 3D extended allocentric headings.

1.2.2 The purpose of Study 2

The neural evidence reviewed above suggests that rats and bats have extended 3D allocentric headings. To specify, the represented allocentric direction on vertical and inverted planes is an extension of the allocentric direction on the ground by pitch rotations. Humans, as mammals and surface-travelling animals, may have a similar cognitive mechanisms as rats to have extended 3D allocentric headings via 90° pitch. However, humans usually have rare locomotion experience with pitch rotations therefore it is also possible that humans do not have full 3D headings.

Study 2 in this dissertation work (Chapter 3) aimed to investigate this question in 3D active locomotion via pitch rotations. Specifically, human participants were tested in updating allocentric heading from horizontal ground to the vertical walls via 90° pitch or to the ceiling via 180° pitch. The findings in Study 2 would shed light on whether there are different updating mechanisms for yaw and pitch rotations in humans.

1.3 Individual difference in navigation

The above sections have reviewed previous research related to 3D location memory and 3D heading representation and also have outlined the purposes of the studies that will be presented in the following chapters. In this section, I briefly review research about individual differences in 3D spatial representation.

Individual difference is a traditional topic in spatial cognition area (Wolbers & Hegarty, 2010). There are three major influences on different performances in spatial tasks. One is evolutionary (phylogenetic) influences across different species. The second is ontogenetic influences; that is, developmental changes across different ages. The third is gender difference, which also possibly interacts with the other two factors.

1.3.1 Evolutionary influences across different species

The priority of horizontal and vertical information has been found to be different for different species. For example, hummingbirds and rats prioritize horizontal and vertical locomotion differently (Flores-Abreu et al., 2014). The animals were trained to learn a rewarded location in a 3D cubic maze and in testing, they searched for that location in the maze. A successful search required encoding both horizontal and vertical information on three dimensions. During testing in the absence of reward, hummingbirds searched horizontally at the height of the rewarded location, which suggests that they processed the vertical information before the horizontal one. By contrast, rats searched up and down relative to the rewarded location, which suggests that they processed the horizontal information before the vertical one. These two species (terrestrial and avian) show different preference for horizontal metric information. Even for species that both are terrestrial animals, there might exist differences. For example, mice, as rodents, are able to simultaneously represent both vertical and horizontal components of a spatial task, but having to encode both components creates difficulties for them (J. J. Wilson et al., 2015), which is different from what has been found among rats who can encode both components at the same time (Flores-Abreu et al., 2014; Grobéty & Schenk, 1992; Jovalekic et al., 2011). Fish, as animals whose navigation includes a substantial vertical component, can encode both horizontal and vertical components through changes in hydrostatic pressure, which is essentially influenced by gravity (Burt de Perera, De Vos, & Guilford, 2005). When the learned horizontal and vertical components of space are placed into conflict with one another, the fish consistently chose the vertical learned direction, which indicates that vertical axis might be a preference for fish (Holbrook & Burt de Perera, 2009). These findings suggest that different species might have developed different neural and cognitive mechanisms to accommodate the natural locomotion style.

Another line of research that may reflect the species differences is reorientation research. The orienting ability on the horizontal plane has been examined thoroughly across different species (for review, see Cheng, Huttenlocher, & Newcombe, 2013; Cheng & Newcombe, 2005). The reorientation paradigm first introduced by Cheng (1986), has been widely used for the study of reorientation in numerous species including humans. Briefly, the subject first learns the location of a reward, which is usually at one corner of a room with geometric properties. The reward is then hidden and the subject is rotated to become disoriented before searching for the reward. Accurate search indicates successful re-orientation. In follow-up studies with this paradigm, researchers have investigated the relative dominance of cues within the reorientation paradigm by training with more than one type of cue during the learning phase. In studies with human children, each cue type is then tested with other cue(s) removed to see whether it was learned and could be used to reorient. In this paradigm, if Cue A is learned at a younger age comparing to Cue B, then Cue A is taken as a more relatively dominant cue. That is, differences in the age at which different cue types are learned have been taken as an indication of the cue's relative dominance. Another way to test the relative dominance is to conduct so-called conflict tests after the learning phase; on these tests the environment is manipulated to place the cues in opposition to one another (for example, after learning in a rectangular room with a red wall (a featural cue) at the short side of the room, in testing wall color is rotated to a long side wall to place the featural cues of wall colors in opposition to the geometric cues from the room shape). The extent to which searching follows each cue type is taken as an indication of that cue's dominance.

Reorientation studies also indicate evolutionary influences on the different performances across individuals. Here I review two typical cues that are with vertical components: height and slope.

Height cue is a typical vertical cue purely from visual modality. For hikers in natural environments, a mountain's peak is usually a salient cue for orientation because it can be seen from even 100 km away and it provides enduring and reliable information about directions in the environment. Humans are able to use vertical wall height as a cue to orient themselves from 4 years old (Du, Spetch, & Mou, 2016; Hu et al., 2015). When pigeons were tested with a similar paradigm and environments, there were different results. When the height cues conflict with room geometry, pigeons preferred the geometry cues over the height cues only when the wall height was not perceptually very salient to them (Du, Mahdi, Paul, & Spetch, 2016).

Slope can also be a useful cue for orientation (Chai & Jacobs, 2010). Herein slope is defined as elevation changes across a surface (e.g. undulating terrain and hills). Slope cues are complex. According to Newcombe and Huttenlocher (2000), slope cannot be exclusively defined in self-referenced or external referenced system, because it provides inputs through multiple modalities (i.e., visual, proprioceptive and kinesthetic modalities), and information from both the horizontal and vertical dimensions (Hu et al., 2015; Nardi, Newcombe, & Shipley, 2011). The ability to use slope alone to reorient has now been shown in human adults, 8-to 10-year-old children, pigeons and rats (C. A. Holmes, Nardi, Newcombe, & Weisberg, 2015; Miniaci, Scotto,

& Bures, 1999; Nardi & Bingman, 2009; Nardi et al., 2011; Nardi, Nitsch, & Bingman, 2010). For example, when pigeons were trained in a sloped trapezoid arena and later tested with the geometric shape of the environment and the slope cue presented in conflict, they primarily used slope (Nardi & Bingman, 2009), suggesting that slope is more heavily relied on by pigeons than the geometric shape of the environment. A subsequent study showed that pigeons relied upon slope even when it was less predictive than the geometric shape of the environment (Nardi et al., 2010). By contrast, not all human adults could spontaneously use the tilted floor to reorient. Some people used the slope cue only when attention was drawn to the slope although the slope was the only available cue in the testing environment (Nardi et al., 2011).

These results may suggest the difference between terrestrial and avian species, at least in the reorientation task. In terms of 3D heading updating, it is possible that comparing with rats and bats, humans have a different mechanism and may not fit the toroidal model (Finkelstein et al., 2015; Taube et al., 2013).

1.3.2 Ontogenetic and individual experience influences

There is another factor that worth taking into account: developmental history. Rearing studies in reorientation research indicates that individual life experience may influence the use of featural cues to orient but not the use of geometry (Batty, Bloomfield, Spetch, & Sturdy, 2009; Brown, Spetch, & Hurd, 2007; Chiandetti & Vallortigara, 2008). In terms of vertical cues, for example, Hu et al. (2015) found that human children could use horizontal geometry to reorient at a younger age than vertical wall height. However, when horizontal geometry and height cues were presented in conflict, human adults did not show a preference for horizontal geometry (Du, Spetch, et al., 2016). The two studies have similar design and testing environments but suggest different dominance of the vertical height cue. Adults do not prefer horizontal cues while children learned to use height cues later than horizontal cues. Such difference may be explained by developmental changes although now we still do not know much about how this transition occurs and what the cognitive mechanisms are behind it.

Furthermore, individual experience, even just before the test, may also play a role. For example, in one of my published work (Du, Spetch, et al., 2016), human adults were tested in both a rectangular room and a rhombus room using a reorientation paradigm. Both rooms had two opposite high walls at equivalent height. In the testing phase, the room shape and the height cue were put into conflict to indicate different correct corners. Participants chose correct corners according to height cues more often in their second testing condition than in their first one. This is due to the fact that participants were more exposed to the height cue and thus the relative salience of height increased in the second environment compared with that in the first environment. This suggests that individual's choice not only depends on their experience in real life but also on the experience in the experimental environments.

1.3.3 Gender differences

Gender differences have found in many spatial tasks (Wolbers & Hegarty, 2010). For example, in 8-year-old children and adults, males showed higher accuracy when using slope to reorient (C. A. Holmes et al., 2015; Nardi et al., 2011). Such differences may be related to task demand, anxiety, hormonal fluctuations, and strategies (Wolbers & Hegarty, 2010). For example, in the reorientation research about the use of slope cue, males were reported to be more confident in their target choice than females (Nardi, Newcombe, & Shipley, 2013).

Gender may interact with the individual history factors to influence individual performances. For example, in studies using virtual reality to present environments, males usually showed better performance than females in spatial tasks (Wolbers & Hegarty, 2010). But such gender differences might disappear if more relevant training experience is given to the participants (Feng, Spence, & Pratt, 2007).

Overall, the factors that cause individual difference may also play a role in 3D spatial representation. The dissertation work will further discuss these factors in Chapter 4 with the findings in the current two studies.

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Chapter 2 When humans can fly: Imprecise vertical localization in human locomotion

2.1 Abstract

Previous research indicates that while animals who locomote on surfaces have a more variable spatial coding vertically than horizontally, animals who fly do not demonstrate a horizontal advantage (Hayman et al., 2011; Yartsev & Ulanovsky, 2013). The current study investigated whether humans' localization is more variable vertically than horizontally in different locomotion modes. In an immersive virtual environment, participants learned the locations of objects presented on one wall of a virtual room. By locomoting from a location on the floor to each object, they collected the objects and then replaced these objects using memories. After their responses, the correct locations were indicated as feedback. During testing, they replaced objects without feedback. One group of participants (the flying group) flew three-dimensionally along their viewing direction by pushing a joystick. The second group (climbing group) locomoted only on the floor and the wall along the projection of the viewing direction onto the current travelling surface. The third group pressed a button to be teleported from the floor to the wall and then locomoted on the wall (teleportation group). The results showed that the variance of localization error was larger vertically than horizontally in the flying and climbing groups but that the pattern reversed in the teleportation group. In addition, while both the flying and teleportation groups locomoted straight towards the target location, the climbing group locomoted straight towards the projection of the target location onto the ground rather than straight towards the wall, indicating that the climbing group tried to avoid horizontal movements on the wall. These results suggest that humans' horizontal advantage of localization is due to spatial encoding, not to more precise horizontal locomotion on the wall.

Keywords: locomotion, 3D space, navigation, localization, spatial memory

2.2 Introduction

Spatial localization is essential to all mobile animals. In both natural and artefactual environments, humans and non-human animals need to remember and locate objects (e.g., food and shelter) in a three-dimensional space. For example, a driver who parks his or her car in a multi-level garage needs to remember and locate the car with information in three dimensions.

Many studies have looked at the spatial memory of different species in the horizontal plane but neglected memories in a three-dimensional space involving both horizontal and vertical components (Jeffery, Jovalekic, Verriotis, & Hayman, 2013; Jeffery, Wilson, Casali, & Hayman, 2015). Some research examined memories in the three-dimensional space and demonstrated that animals may have a horizontal memory advantage when both horizontal and vertical information about the locations is required. Neuroscience findings indicate that place cells of rats have a larger firing field vertically than horizontally (Hayman, Verriotis, Jovalekic, Fenton, & Jeffery, 2011). This suggests that rats may encode the vertical component of space with larger errors than the horizontal component.

Based on this evidence, a theory has been proposed. It states that spatial representation in three-dimensional world seems to be a set of 2D, planar encoding rather than 3D, volumetric encoding (Jeffery et al., 2013, 2015). According to this theory, the horizontal advantage in spatial memory is caused by non-equal encoding mechanisms for spatial information in horizontal and vertical dimensions.

However, not all animals demonstrate the horizontal advantage. Neuroscience research suggests that when bats flew through a 3D volumetric space, the firing fields of place neurons were not compressed or elongated in either dimension, unlike what was found in rats (Yartsev &

Ulanovsky, 2013). In other words, for flying bats, the vertical and horizontal components of space appear to be encoded with equal errors.

One explanation for this discrepancy across studies is the different locomotion modes of the animals used in these studies. Rats and mice navigated on surfaces whereas bats navigated three-dimensionally in these studies. If we assume that locomotion is much more difficult vertically than horizontally when animals navigate on surfaces, then we would expect that localization vertically is more variable, showing a horizontal advantage for rats and mice. If we further assume that locomotion is not harder vertically than horizontally when animals fly, then we would expect no horizontal advantage for bats. Therefore, the horizontal advantage is possibly due to more precision in horizontal locomotion than vertical locomotion on a vertical plane. We refer to this explanation as the locomotion-mode-specific hypothesis. Furthermore, the locomotion mode might affect localization because animals may have difference preferences for horizontal and vertical movements. For example, rats prioritize horizontal over vertical movements on a vertical pegboard (Jovalekic et al., 2011), whereas non-surface-based animals do not have such preferences (Flores-Abreu, Hurly, Ainge, & Healy, 2014; Holbrook & Burt de Perera, 2009). If we assume that location memory decays significantly during locomotion, then the horizontal advantage appears for the animals who locomote horizontally first on a surface but does not appear for the animals who fly. Note that in this study, the “locomotion mode” in locomotion-mode-specific hypothesis refers to the traveling manner of an individual in a specific traversed path, not the natural traveling manner in the individual’s history. In particular, it refers to the traveling manner that was manipulated in this study (flying or surface-based locomotion).

Another possible explanation for the horizontal advantage is that it is species-specific and relevant to evolutionary reasons. Naturally, rats and mice are capable only of surface-based locomotion whereas bats fly. To accommodate their locomotion modes in the natural environment, different species have developed different cognitive and neural mechanisms for location memories. In particular, the species (e.g., rats and mice) that navigate on surfaces encode locations more precisely in the horizontal dimension than in the vertical dimension because they are much more likely to navigate horizontally than vertically. In contrast, the species (e.g., bats) that fly in the air encode locations as precisely in the horizontal dimension as in the vertical dimension because they need to navigate both horizontally and vertically in flying. We refer to this explanation as the species-specific hypothesis.

The previous studies did not independently manipulate locomotion modes and species, and as a result could not distinguish between these two hypotheses. In these studies, the locomotion modes used in the studies depended on species. In particular, in the studies rats always locomoted on surfaces whereas bats always flew in the air. To distinguish between the two hypotheses, we should examine the horizontal advantage in localization by using the locomotion mode that is not aligned with the natural locomotion of the tested species. For example, we might test a flying rat. If a flying rat still showed the horizontal advantage, then the species-specific hypothesis would be supported. If a flying rat did not show the horizontal advantage, then the locomotion-mode-specific hypothesis would be supported.

The first purpose of the current study is to investigate whether humans' localization is less variable horizontally than vertically in flying and surface-based locomotion modes. In nature, humans usually navigate on surfaces. However, in an immersive virtual environment, human participants can perform both surface-based and non-surface-based locomotion. In particular, participants learned targets' locations on the wall while standing on a location on the floor, then replaced the targets in the original locations based on memories by flying or locomoting on surfaces. Therefore, the species-specific hypothesis predicts that regardless of the locomotion mode used in the experiment, humans' localization would be less variable horizontally than vertically because humans are surface-based species. In contrast, the locomotion-mode-specific hypothesis predicts that humans' localization would be less variable horizontally than vertically only in the surface-based locomotion mode but comparable horizontally and vertically in the flying mode. Since locomoting in the virtual environment is not a natural way to locomote for all participants, we added a practice phase before the formal experiment for both the flying and surface-locomotion groups. The practice phase was designed to eliminate the influence of familiarity to different locomotion modes and familiarity to the virtual environment.

Both hypotheses predict that the participants who did surface-based locomotion in the experiment would demonstrate a horizontal advantage. According to the species-specific hypothesis, humans, as surfaced-travelling animals, might have the horizontal advantage in spatial coding (Jeffery et al., 2013, 2015). The locomotion-mode-specific hypothesis also predicts the horizontal advantage as long as humans navigate on surfaces because horizontal locomotion is more precise than vertical locomotion on a vertical plane. This prediction is consistent with most of the findings in the previous human studies. Some evidence from previous studies suggests that humans treat horizontal and vertical spatial information differently. Humans tend to underestimate the angle through which they move in the horizontal plane. However, either no bias or an overestimation of the movement angle is found in the sagittal plane, which suggests that the human path integration system might operate differently in all three dimensions (Barnett-Cowan, Meilinger, Vidal, Teufel, & Bülthoff, 2012). In multi-floored environments, humans showed better memories about the routes along each level of floors than those along columns across floors (Dollé, Droulez, Bennequin, Berthoz, & Thibault, 2015; Thibault, Pasqualotto, Vidal, Droulez, & Berthoz, 2013). Some fMRI studies in humans suggest that the neural representations of the cardinal axes of motion (horizontal and vertical) are partially distinct, at least in conditions in which the motion information was visually presented (Indovina et al., 2013, 2016).

Furthermore, it has been found that humans may have horizontal biases. For example, humans have a tendency to overestimate height relative to egocentric distance (Higashiyama & Ueyama, 1988; Li, Phillips, & Durgin, 2011). However, one recent study showed that spatial memories of a layout of objects presented on horizontal- and vertical-oriented boards are comparable (Hinterecker et al., 2017). It is not clear whether this finding can be used to directly examine the horizontal advantage. Although the horizontal-oriented board has two horizontal dimensions, the vertical-oriented board used in Hinterecker et al. (2017) had one horizontal dimension. The horizontal dimension of the vertical-oriented board might reduce or eliminate the accuracy differences between spatial memories of these two boards. Therefore, it is still important to examine whether there is a horizontal advantage for human localization although both of our hypotheses predict this.

These two hypotheses had different predictions on the horizontal advantage for the participants who flew. According to the locomotion-mode-specific hypothesis, the flying group, different from the surface-based locomotion group, would not demonstrate a horizontal advantage because vertical and horizontal locomotion were comparable during flying. For example, translations (i.e., movements in straight lines) in both horizontal and vertical dimensions would be presented by visual cues in the virtual environment. According to the species-specific hypothesis, the flying group, same as the surface-based locomotion group, would also demonstrate a horizontal advantage effect because humans are surface-based animals in nature and spatial coding is more precise horizontally than vertically for surface-based animals. Therefore, the results of the flying group could help to distinguish between these two hypotheses.

As mentioned above, surface-based animals (e.g., rats) prioritize horizontal over vertical movements on a vertical pegboard (Jovalekic et al., 2011), whereas non-surface-based animals such as birds and fish do not have such a preference (Flores-Abreu et al., 2014; Holbrook & Burt de Perera, 2009). It is not clear whether human participants prioritize horizontal over vertical movements on a vertical plane. In addition, when participants locomote on the ground before reaching the wall, they can still choose to locomote straight to the wall in the shortest distance or to locomote straight to the horizontal location of the target (i.e., the projection of the target location onto the floor). As a consequence, they still move both vertically and horizontally on the wall if they locomote straight to the wall in the shortest distance whereas they only need to move vertically on the wall if they locomote straight to the horizontal location of the target. For these reasons, the second purpose of the current study is to examine which locomotion route is preferred by humans in surface-based locomotion: i.e., whether they would choose the moving trajectory only on the wall or the moving trajectory both on the ground and on the wall.

To answer this question, we recruited two surfaced-based groups in addition to one flying group. Both groups learned targets presented on the wall while standing on the ground. One group was teleported to the wall and started their locomotion from a location at the bottom of the wall whereas the other group started their locomotion from a location on the ground. We recorded their locomotion trajectories to examine whether the former group preferred locomoting horizontally first on the wall and whether the latter group preferred locomoting straight towards the wall or towards the horizontal location of the target (i.e., the projection of the target location onto the ground) on the ground.

To summarize, in the current study, we asked participants to navigate in a virtual reality environment in different locomotion modes (flying and surface-based climbing). There were three groups in the current study: flying, climbing and teleportation. The flying group had a different locomotion mode from the other two groups; participants could move freely three-dimensionally like birds. Both the climbing and the teleportation groups locomoted only on surfaces (on the ground or on the wall). However, the teleportation group was only allowed to move on the wall (horizontally and/or vertically) as they were teleported to the bottom of the wall before locomoting to the target location. For the climbing group, we predicted a horizontal advantage effect in localization. For the other two groups, we did not have predictions in specific directions. The results in the flying group would help us to differentiate the locomotion-mode-specific and the species-specific hypotheses. The locomotion trajectories of the teleportation group could examine whether humans prioritize horizontal movements on vertical surfaces.

2.3 Method

2.3.1 Participants

Seventy-two university students participated in the experiment (age range = 17–24 years, *M* = 19.35 years). The participants were assigned equally into three groups (flying, climbing and teleportation groups) with an equal number of each gender. Prior power analysis showed that the power would be 0.76 assuming a strong effect size (Cohen’s $d = 0.8$), an α error of 0.05, and a sample size of 24 participants.

2.3.2 Apparatus and environment

The experiment was conducted in a 4 × 4 m physical room. The experimental environment was presented to the participants by a virtual reality system that used Vizard software (WorldViz, Santa Barbara, CA), an nVisor head-mounted display (HMD, NVIS, Inc., Reston, VA), and an InterSense-900 motion-tracking system (Billerica, MA). Screen resolution within the display was 1,280 × 1,024 pixels. The horizontal field of view (FOV) was 44° and the vertical FOV was 35°. Participants' physical viewing orientation was tracked by the IS-900 motion-tracking system so that the participants could physically rotate their body to change their viewing orientation in the virtual environment.

A joystick (Logitech ATK3, Logitech, Newark, CA) was used for translational navigation in the virtual environment. The travel direction was determined by participants' viewing orientation. (For details about each group, see the following sections.)

The experimental environment was a rectangular virtual room with different-colored walls (pink, yellow, green, and blue, see Figure 2.1 and the videos in supplementary materials). The room was 15 m wide, 50 m long, and 15 m in height. The walls had a texture designed to increase the perceived optic flow during navigation. For simplicity, in this paper, we use north, south, east, and west to distinguish the walls. During the experiment, participants were never instructed with these terms. The ceiling was light grey with the pattern of square textiles. There was no landmark cue in the environment.

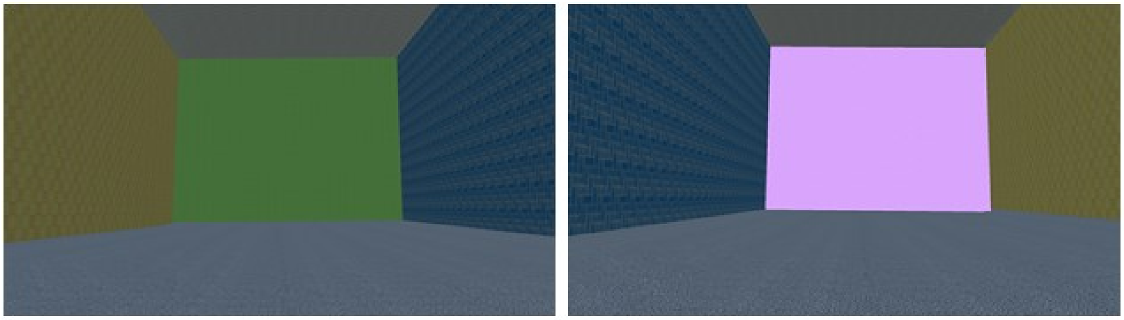

Figure 2.1. Screenshots of the experimental environment. These show the scenes when a participant was standing in front of the opposite wall on the ground at a height of 1.5 m.

2.3.3 Materials and design

Participants were tested individually and were randomly (with equal males and females) assigned into one of the three groups: flying, climbing, or teleportation. The only difference between the groups was the locomotion mode which is the primary independent variable. The flying group could navigate three-dimensionally by pushing the joystick and locomoting along their viewing direction. The climbing group could travel only on surfaces by pushing the joystick and locomoting along the projection of their viewing direction onto the current travelling surface. When participants were at the intersection of two planes, they could move to the plane that they were looking at by pushing the joystick (see supplementary material for exemplar videos). The locomotion mode for the teleportation group was the same as that for the climbing group except that the participants did not navigate across the floor to reach the target wall. Instead, on every trial, they were teleported from a location on the floor to the bottom of the target wall directly by clicking a button on the joystick. The new location after the teleportation was the projection of the original location onto the target wall.

Each participant learned and replaced four layouts of objects presented on the walls in four blocks. In each block, they learned and replaced one layout. The first block of learning and replacing was for practice so that participants became familiar with using the joystick to replace objects on the wall. The four layouts used the same objects (a bottle, a lock, a candle, and a piece of wood) but different sets of locations. For each layout, the association between targets and locations was randomly determined for each participant. Assigning the four layouts to the four blocks was counterbalanced across participants in a Latin-square order for each gender. Within one block, the target objects were presented sequentially on the same wall (either north wall or south wall). Across blocks, the layouts were presented alternately on two opposite walls (either the north wall or south wall, both in a 15 × 15 m square shape). The participants were informed which wall was the target wall in each block.

As in previous studies, there were three phases in each block: the pick-up phase, learning phase, and testing phase (Doeller & Burgess, 2008). In the pick-up phase, participants picked up the four targets that were sequentially presented. In the learning and testing phases, participants used their memories to replace the four targets probed in a sequence. The correct location of the object was presented for feedback after participants responded to each object in the learning phase. There was no feedback in the testing phase. In the learning phase, there were four trials in total, one for each object. The order was randomly determined. In the testing phase, there were four blocks of trials that included each of the four objects in a randomized order within each block. Consequently, for each participant, across the three experimental blocks, there were 48 trials in the testing phases.

For each testing trial, the replaced location of the target was recorded. Each participant's moving trajectory between the beginning of each trial and the time point at which the object was placed on that trial was also recorded by recording each participant's head location every 50 milliseconds (ms).

2.3.4 Procedure

Participants were led into the experiment room blindfolded. After putting on the headset, participants saw the experimental room in a virtual environment. First, they practiced using the joystick to navigate in the environment. For the climbing and the teleportation groups, the practice included moving on the walls horizontally and vertically. Then participants started the practice block, followed by three experimental blocks. Each block contained a pick-up phase, a learning phase, and a testing phase.

In the pick-up phase, participants were teleported to a random location on the floor before each of the four target objects was presented. They navigated to the target location and picked up the object when their head location and the target's location were closer than 0.5 m. Once they collected all four objects, they proceeded to the learning phase. For each trial in the learning phase, the participants were teleported to a random location on the floor before one probed target began spinning at the bottom right corner of the screen. Participants navigated to the target wall and clicked a button on the joystick to replace the object at the projection of their head position onto the wall. After the response, the correct location was shown to the participants again as feedback and participants then navigated towards the correct location from the response location. For each trial in the testing phase, participants started from the random location and then replaced the probed object to the original location as in the learning phase but did not receive any feedback.

2.4 Results

For each testing trial and each participant, we calculated the horizontal distance error (the horizontal distance between the response location and the correct location) and vertical distance error (the vertical distance between the response location and the correct location). For simplicity, we define the horizontal axis on the target wall as the x axis and the vertical axis on the target wall as the y axis. We define the directions of Up and Right as positive. Preliminary analyses revealed that block and gender had no effect on the signed horizontal or vertical distance errors (*p*s > .12). As a result, data were collapsed across these factors in subsequent analyses.

The signed distance error as a function of dimension (horizontal, vertical) and group (flying, climbing, teleportation) is plotted in Figure 2.2. In general, mean signed distance errors were small and in most cases within 0.3 m, which were very small compared to the width and height of the target wall (15 × 15 m). To examine whether the participants had a general horizontal or vertical bias in the responses towards one direction, we compared the signed horizontal and vertical errors for each group with 0 using one-sample *t* tests. The results showed that only the horizontal error in the flying group was significantly biased towards the left [$t(23) = 3.03$, $p = .006$, Cohen's $d = 0.87$; other *p*s > .05].

To examine the horizontal advantage in localization, we used the standard deviation (SD) of the signed distance errors to examine the variability of the responses in the horizontal and vertical dimensions. The SD of error as a function of dimension (horizontal, vertical) and group (flying, climbing, teleportation) is plotted in Figure 2.3. A 3 × 2 mixed ANOVA (Group [Flying, Climbing, Teleport] × Dimension [Horizontal, Vertical]) with SD as the dependent variable was conducted. There was a significant main effect of Group, $F(2, 69) = 5.02$, $p = .009$, $\eta_p^2 = .13$, $MSE = 1.12$. The main effect of Dimension was not significant, $F(1, 69) = 1.94$, $p = .168$, $\eta_p^2 = .03$, $MSE = 0.11$. The interaction between the two factors was significant, $F(2, 69) = 6.54$, $p = .003$, $\eta_p^2 = .16$, $MSE = 0.11$.

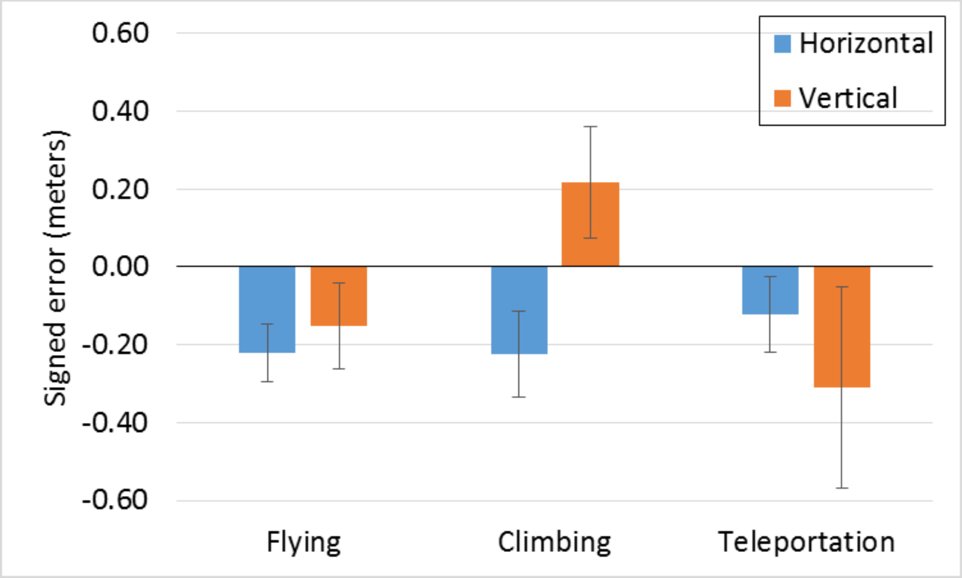

Figure 2.2. Signed distance errors for the flying, climbing, and teleportation groups. Blue bars represent horizontal errors. Orange bars represent vertical errors. Error bars represent the standard errors of the mean.

To further interpret the interaction, *t* tests were conducted separately for each group[2]. The results showed that both the flying and climbing groups were significantly less variable in the horizontal dimension than in the vertical dimension [flying: $t(69) = 2.42$, $p = .018$; climbing: $t(69) = 2.14$, $p = .036$], which suggests the horizontal advantage found in previous animal studies. However, the teleportation group showed a larger variance in the horizontal dimension than in the vertical dimension, $t(69) = 2.14$, $p = .036$, which suggests a vertical advantage.

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[2] Note that the *t* tests conducted here used the MSE from the ANOVA, not the MSE from each paired t test (which would not consider the third group). Therefore, *df* corresponds to the MSE in ANOVA, not that in a regular *t* test. The regular *t* tests were not used because the actual purpose of these t tests is to do a simple analysis for the interaction effect. Therefore, although only two groups were compared in a t test, the variability caused by the third group should also be considered. For examples of this method, please see Mou & McNamara (2002) and Mou, McNamara, Valiquette, & Rump (2004).

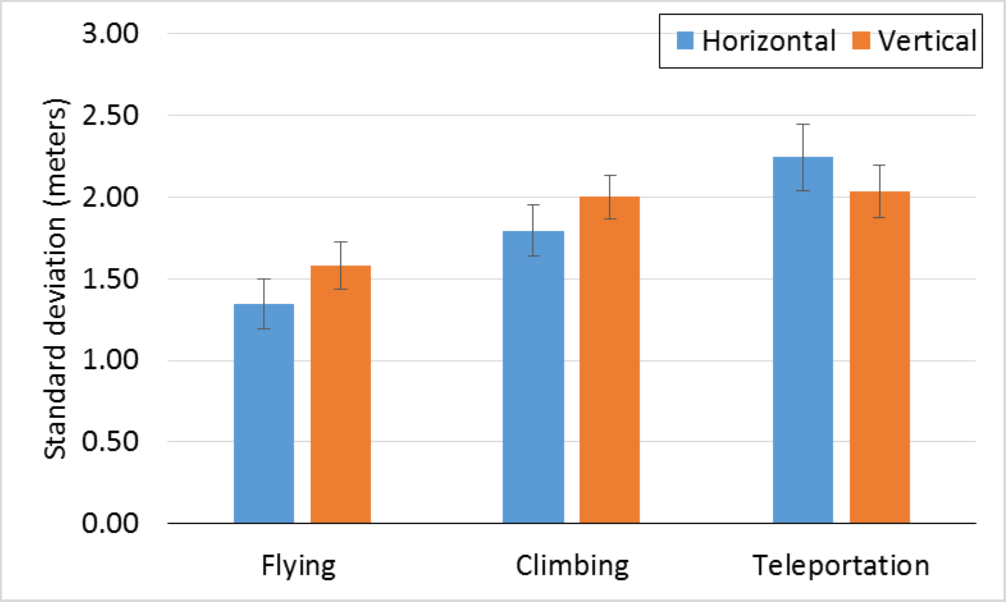

Figure 2.3. Standard deviations (SD) of signed distance errors for flying, climbing, and teleportation groups. Blue bars represent SD of horizontal errors. Orange bars represent SD of vertical errors. Error bars represent the standard errors of the mean.

We analyzed the trajectory information (i.e., participants' head positions, x and y) during the participants' locomotion in each testing trial. Note that the starting position on each trial was randomly determined. Therefore, the horizontal movement distance (i.e., x) at each time point (every 50 ms) was calculated as the absolute distance between each participant's current position and the starting position in the horizontal dimension. Similarly, the vertical movement distance (i.e., y) at each time point was also calculated as the absolute distance between each participant's current position and the starting position in the vertical dimension. The distance to the wall (i.e., z) was not analyzed as all participants knew the target wall and moved towards it.

Figure 2.4 shows the absolute distance from the starting position to the current location as a function of time percentage (e.g., 0 is the starting point, 1 is the time point of the placement response) in both the horizontal (x) and vertical (y) dimensions for three groups, respectively. As

Figure 2.4 clearly shows, the participants in the three groups displayed different movement patterns although the total travel distances in both the horizontal (x) and vertical (y) dimensions for the two groups were not different. The climbing group showed clear “turning points” on the curves, which was the time point when they reached the wall. When climbing group was on the floor, the participants locomoted towards the projection of the target onto the floor so that only the horizontal (x) distance increased before they reached the wall. After they reached the wall, they seemed to maintain basically the same horizontal coordinate (x) and locomote only vertically (i.e., y) until they placed the object to finish that trial. By contrast, the flying group locomoted straight towards the target so that both the horizontal (x) and vertical (y) distances increased at the same time until they reached the target wall and placed the object. Since the teleportation group was not allowed to locomote on the ground, we examined only the trajectory after the participants were teleported to the wall. Like the flying group, the teleportation group also locomoted straight towards the target so that both the horizontal (x) and vertical (y) distances increased simultaneously until the participants placed the object.

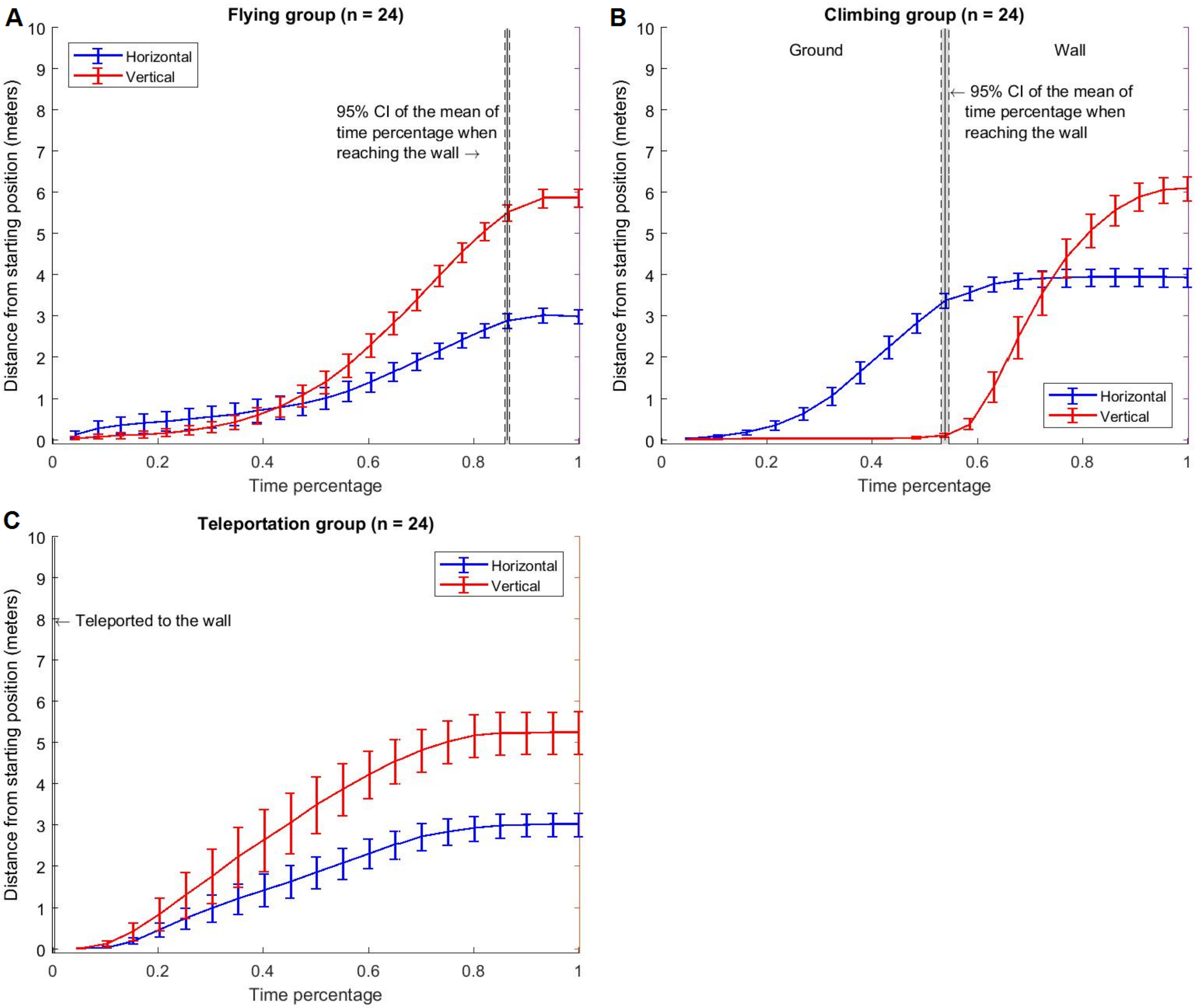
A
Flying group (n = 24)
Horizontal
Vertical
95% CI of the mean of
time percentage when
reaching the wall →
Distance from starting position (meters)
Time percentage
0
1
2
3
4
5
6
7
8
9
10
0
0.2
0.4
0.6
0.8
1
B
Climbing group (n = 24)
Ground
Wall
← 95% CI of the mean of
time percentage when
reaching the wall
Horizontal
Vertical
Distance from starting position (meters)
Time percentage
C
Teleportation group (n = 24)
Horizontal
Vertical
← Teleported to the wall
Distance from starting position (meters)
Time percentage

Figure 2.4. Absolute distance from the starting position in the flying (Panel A), climbing (Panel B) and teleportation groups (Panel C). The x axes correspond to the time percentage from the beginning to the end of a trial, from left to right. Blue curves represent the horizontal distance. Red curves represent the vertical distance. Error bars represent 95% confidential intervals in each time section.

2.5 Discussion

The current study examined humans' object localization in both horizontal and vertical dimensions. There are two important findings. First, the localization variance was larger vertically than horizontally in both the flying and the climbing groups, which reflects a horizontal advantage. However, the teleportation group showed a vertical advantage. Second, the participants locomoted straight towards the target location without prioritizing the horizontal movement while flying (flying group) or locomoting only on the wall (teleportation group). The climbing group locomoted towards the horizontal location of the target (the projection onto the floor) while locomoting on the ground.

Both the flying and climbing groups showed a horizontal advantage in localization, suggesting that the locomotion mode (flying or surface-based locomotion) may not be the crucial factor that led to the horizontal advantage in the previous studies (Hayman et al., 2011). As the flying group could see the edges of the wall and the target object at the same time in the pick-up and learning phases with minimum movement difficulty, they should have encoded the locations relative to both the vertical and horizontal edges of the wall. Therefore, in the testing phase, they could have determined the goal location using the edges of the wall. Since they could fly to the goal location by looking at it, the flying locomotion per se should not have produced the horizontal advantage. This suggests that the horizontal advantage in the flying group is more likely to come from encoding rather than locomotion. Furthermore, the climbing group showed the same degree of horizontal advantage as the flying group despite their very different locomotion modes. It is hard to believe that both groups showed the horizontal advantage because one specific locomotion mode intrinsically resulted in more precision horizontally than vertically.

These results support the species-specific hypothesis and are not in agreement with the locomotion-mode-specific hypothesis. Regardless of the locomotion mode, humans naturally have a horizontal advantage in spatial memory. Humans, as a surface-based species, locomote mostly on the ground and occasionally vertically in the natural environment (e.g., climbing a mountain). As a consequence, their neural and cognitive systems are developed to accommodate this locomotion style. Specifically, their spatial memories of locations are more precise horizontally than vertically.

One might argue that the flying locomotion mode in the current study might be less familiar to the participants (as humans naturally do not fly in real life without any tools) and thus the horizontal advantage found in the flying group might be due to our specific experimental design in the virtual environment. However, we found that across blocks there was no difference in the SDs. This suggests that although participants were more exposed to the flying locomotion mode in later blocks, their localization was as precise as in the first experimental block. Similar results were found in the other two groups. These results indicate that more exposure to a specific locomotion mode did not lead to more precise localization performance. For this finding, there are two possible explanations. First, humans might have a quick learning or accommodation mechanism intrinsically. At the beginning if the current study, the participants were familiar with the climbing mode and how to localize targets in that mode but unfamiliar with the flying mode. In the practice phase, they learned how to "fly" so they could had quickly accommodated the cognitive mechanism for the usual locomotion mode (surface-based locomotion) to the new flying mode. Therefore, for the same species (humans), the underlying cognitive mechanisms for localization in different locomotion modes (flying vs. surface-based locomotion) might be different. Human body may affords some movements more easily than others. Our brain might have evolved to have a locomotion affordance for these easier movements like the visual affordance mechanism for our visual system (Gibson, 1986). Second, although the participants do not fly in real life, humans might have an intrinsic, common cognitive mechanism prepared for actions in different locomotion modes. The current study used a virtual environment which might be unfamiliar to some of the participants. In the practice phase, the participants quickly learned how to "fly" and how to perform surface-based locomotion using the intrinsic, common mechanism. In other word, the participants just activated the mechanism in order to localize targets in the virtual environment. Clearly, the current study may not be able to discriminate the two possibilities but in future research, they could be dissociated by examining the differences in brain activation in both locomotion modes.

Although the horizontal advantage in spatial coding is species-specific rather than locomotion-specific, locomotion mode also affects localization precision in horizontal and vertical dimensions. In contrast with the climbing group, the teleportation group showed a vertical advantage in localization. In the pick-up and learning phases, all groups of participants viewed the target from a position on the ground; consequently, the vertical advantage in the teleportation group should not have been due to encoding but due to locomotion. In particular, locomotion on the wall might be harder horizontally than vertically. We note that the possible influence of locomotion in localization should not be considered when arguing for the locomotion-mode-specific hypothesis. Instead, the vertical advantage in the teleportation group was inconsistent with the locomotion-mode-specific hypothesis as it attributes the horizontal advantage to more precise locomotion horizontally than vertically on a vertical surface.

The previous studies showed that surface-based animals prioritize horizontal movement while locomoting on the vertical plane (Jovalekic et al., 2011). However, the teleportation group did not show any prioritized horizontal movement. Instead, the group moved towards the target in a straight line (see Figure 2.4C). This kind of pattern was also observed in the flying group (Figure 2.4A). This suggests that human participants might show their preference for a shorter distance by moving straight towards the target location rather than prioritizing horizontal movement. The pattern might be also caused by the difference in testing environments. Our vertical testing surface was a continuous surface whereas Jovalekic et al. (2011) used a vertical pegboard with many horizontal pegs. Such differences in experimental environments might lead to the differences in trajectories. It has been found that experimental design and procedure may also result in different locomotion preferences. For example, when the food's location was fixed across trials and thus the navigation was goal-directed, rats first identified the vertical coordinate and then navigated to the horizontal place (Grobéty & Schenk, 1992). However, when the food's location was not fixed and the navigation was freely foraging, the rats preferred to forage horizontally before doing so vertically (Jovalekic et al., 2011). Therefore, future research should consider these factors in experimental design to compare with other studies.

Interestingly, the climbing group actually chose to locomote towards the horizontal location of the target on the ground and then locomoted only in vertical dimension on the wall, although the participants could choose to locomote in a straight line towards the wall and then towards the target with both the horizontal and vertical distance changes on the wall. These two options did not lead to different total travelling distances. Thus, in addition to preferring to move straight towards the target for the sake of a shorter travelling distance, the participants might have avoided horizontal movements on the wall. If the participants moved straight towards the wall, they would have moved horizontally as well as vertically on the wall. Participants could have been avoiding horizontal movements on the wall due to the difficulty in locomoting horizontally on the wall as suggested by the larger horizontal rather than vertical localization variance in the teleportation group. In addition, when participants moved towards the target's horizontal location, they indeed moved in a natural way of locomotion on the horizontal plane. Therefore, it is not surprising that participants preferred moving towards the target location's projection and avoiding the horizontal locomotion on the wall.

In conclusion, the current study examined humans' spatial localization in 3D navigation. The results demonstrated the horizontal advantage of location memory but vertical advantage of locomotion on a vertical surface. Our results suggest that the locomotion mode does not account for the horizontal advantage for surface-travelling animals. Therefore, the horizontal advantage is more likely to be species-specific rather than locomotion-mode specific.

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Chapter 3 Up is up and north is north: Updating allocentric headings during 3D locomotion in humans

3.1 Abstract

Previous neuroscience studies using rats and bats suggest that the rats' and bats' represented headings on vertical and inverted surfaces are an extension of their headings on the ground by pitch rotations. The current study investigated whether humans can spontaneously extend their allocentric heading on the ground when locomoting to walls and the ceiling. In immersive virtual reality environments, participants first learned a layout of objects on the ground. In testing phases, they initially faced south (or north) and navigated to testing planes: south (or north) walls with the testing heading of Up, or the ceiling with the testing heading of North (or South). They then either replaced the objects on that plane or did a Judgement of Relative Direction (JRD) task ("imagine standing at object A, facing B, point to C") with imagined headings of south and north. The results from the object placement task showed that the participants more likely treated Up on two opposite walls as the same heading, and treated the same direction (e.g., North) on the ceiling and on the ground as the same heading. Only a small portion of participants (about 20%) treated the same directions on the ground and on the ceiling as two opposite headings, indicating that they extended their allocentric heading through pitch rotations. The results of the JRD task showed that only these "extension" participants showed a reversed sensorimotor alignment effect; that is, they delivered a better performance when the imagined facing direction on the ground and the physical facing direction on the ceiling were opposite and not when they were the same. These results indicate that on a behavioral level, only a small portion of humans can spontaneously represent 3D allocentric headings (i.e., pitch) while most humans only represent 3D allocentric directions (e.g., North, Up).

Keywords: spatial orientation, three-dimensional, heading, navigation, reference frame

3.2 Introduction

Spatial orientation is essential to navigation for all mobile animals. To establish ones' orientation, individuals need to determine the relationship between their body and the environment. Usually, the allocentric reference directions in the environment (e.g., cardinal directions) are required during this process because the body-based or egocentric reference system (e.g., front, back, left, right) may not be useful. For example, to guide a friend to navigate over the phone, using language like "facing your left side, go forward" is probably not a good idea. Allocentric reference system is also often termed as "the world's coordinates".

On the horizontal plane, one's orientation relative to the allocentric reference directions (e.g., north) is termed as the allocentric heading (Klatzky, 1998). In other words, the allocentric heading refers to the relationship between their body front-back axis and the environment. Navigating on the horizontal plane, individuals change their allocentric heading by rotating around the head-foot axis of their body (i.e., yaw). For example, individuals who initially faced north could change their allocentric heading from north to east by *yaw* right 90°. Hence, yaw rotations can specify the allocentric heading on the horizontal plane. Many studies have shown that animals including humans can update their allocentric heading in yaw rotations while the animals locomote within the horizontal plane (e.g., Etienne, Maurer, & Séguinot, 1996; Waller, Montello, Richardson, & Hegarty, 2002).

Space is three-dimensional. In addition to the reference directions on the horizontal plane, there are two vertical reference directions (i.e., gravity up and down, or floor to ceiling and ceiling to floor). Although there are many studies investigating how humans update allocentric headings on the horizontal plane, studies examining how humans represent and update their 3D allocentric headings are rare. To specify, 3D allocentric headings are the rotational transformation relations between ones' all three body axes (front-back, left-right, up-down) and the allocentric reference directions (north-south, east-west, gravity up-down). The rotational transformation relations include yaw (rotation around the up-down axis of a human body), pitch (rotation around the left-right axis of a human body), and roll (rotation around the front-back of a human body) (for a review about these three types of rotations, see Jeffery, Wilson, Casali, & Hayman, 2015). We also define 3D allocentric facing direction as the rotational transformation relations between ones' front-back axis and the allocentric reference directions. Note that the allocentric heading and the allocentric facing direction of an upright individual on the horizontal plane are equivalent. However, 3D allocentric headings of individuals cannot be specified by individuals' facing directions. For example, an upright person facing north has the same 3D allocentric facing direction as an upside-down person facing north (Figure 3.1). For both persons, the relations between their front-back body axes in terms of the allocentric directions are the same. However, an upright person facing north has the different 3D allocentric heading from an upside-down person facing north. The former needs to roll 180° (or yaw 180° and then pitch 180°) to have the same heading as the latter.

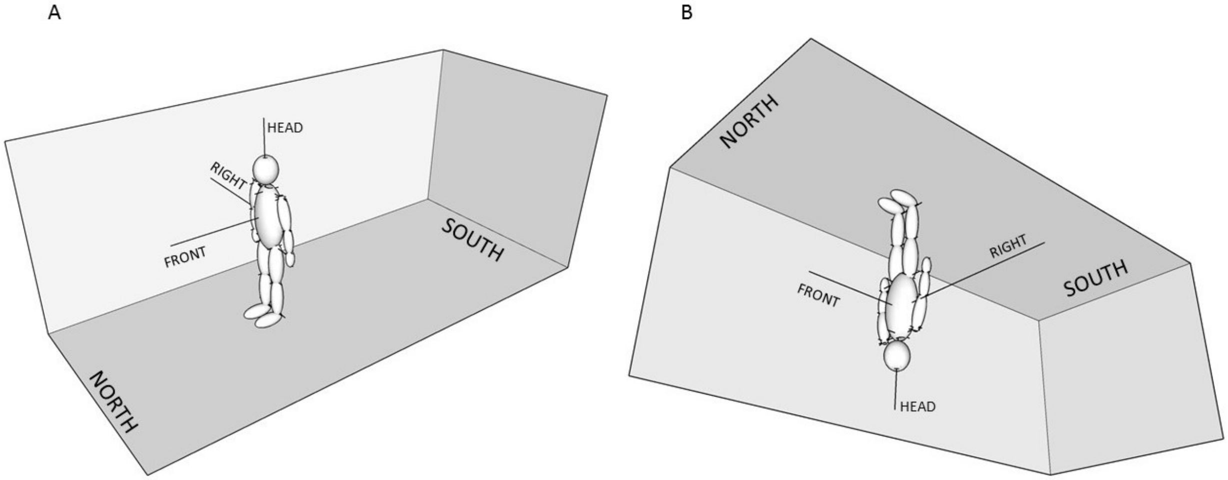

Figure 3.1. 3D allocentric heading and 3D facing direction. Panel A shows a person who is standing upright on the horizontal ground and facing north. Panel B shows the person who is on the ceiling upside down and facing north. In both situations, the individual will have the same facing direction as the individual's body front-back axis always points to north in respect to the allocentric directions (i.e., in the world's coordinates). However, the left-right and head-foot axes point to different allocentric directions. Therefore the individual will have different 3D allocentric headings in these two situations.

While humans mostly make yaw body rotations in the environment, other animals might also engage other kinds of rotations (i.e., pitch or roll) in navigation. For example, when a rat locomotes from the horizontal ground to a vertical wall, it will perform a pitch up 90° rotation. Bats may pitch 180° to hang upside down on the ceiling of a cave. Some more recent research in neuroscience examined whether animals can update the heading representation in three-dimensional space (Jeffery, Jovalekic, Verriotis, & Hayman, 2013; Jeffery et al., 2015). In these studies, animals do pitch rotations in addition to yaw rotations and the changes in the head direction cells' firing are taken as indicators to the extended representation. For example, when rats climbed onto vertical walls from a horizontal plane, the head direction cells maintained the same firing patterns as if the walls were an extension of the floor (Calton & Taube, 2005; Stackman, Tullman, & Taube, 2000; Taube, Wang, Kim, & Frohardt, 2013). When flying bats performed pitch rotation movements in all 360°, the movements did not affect the head direction cells' firing patterns (Finkelstein et al., 2015). These studies suggest that for these animals, the represented allocentric direction on vertical and inverted planes is an extension of the allocentric direction on the ground by pitch rotations. For example, flying bats have a toroidal coordinate system; therefore pitch rotation movements do not affect the azimuth head direction cells' firing patterns (Finkelstein et al., 2015).

According to this toroidal model, an extension hypothesis is shown in Figure 3.2. If the animal locomotes to the vertical planes via a pitch rotation (e.g., from the ground to the walls), head direction cells treat the vertical plane as an extension of the allocentric reference directions (e.g., cardinal directions) on the floor rotated by the 90° pitch up. As a result, the direction *up* on the north wall is the extension of the *north* on the ground whereas *up* on the south wall is the extension of the *south* on the ground. If the animal locomotes to the inverted plane (e.g., ceiling), head direction cells treat the ceiling as an extension of the allocentric reference directions on the floor rotated by the 180° pitch up. Consequently, the direction *north* on the ceiling is *south* on the floor. A dual-axis model has been proposed recently account for locomoting between two vertical walls (Page, Wilson, & Jeffery, 2018). According to this theory, if the animal locomotes via pitch rotation across vertical walls, the head direction cells' firing will change, which is different from what is predicted by the toroidal model. However, these two models are identical if animals only travel between horizontal and vertical planes. As in the current study, participants only locomoted between horizontal and vertical planes, we do not differentiate these two models and use the extended-allocentric-heading hypothesis to refer to both.

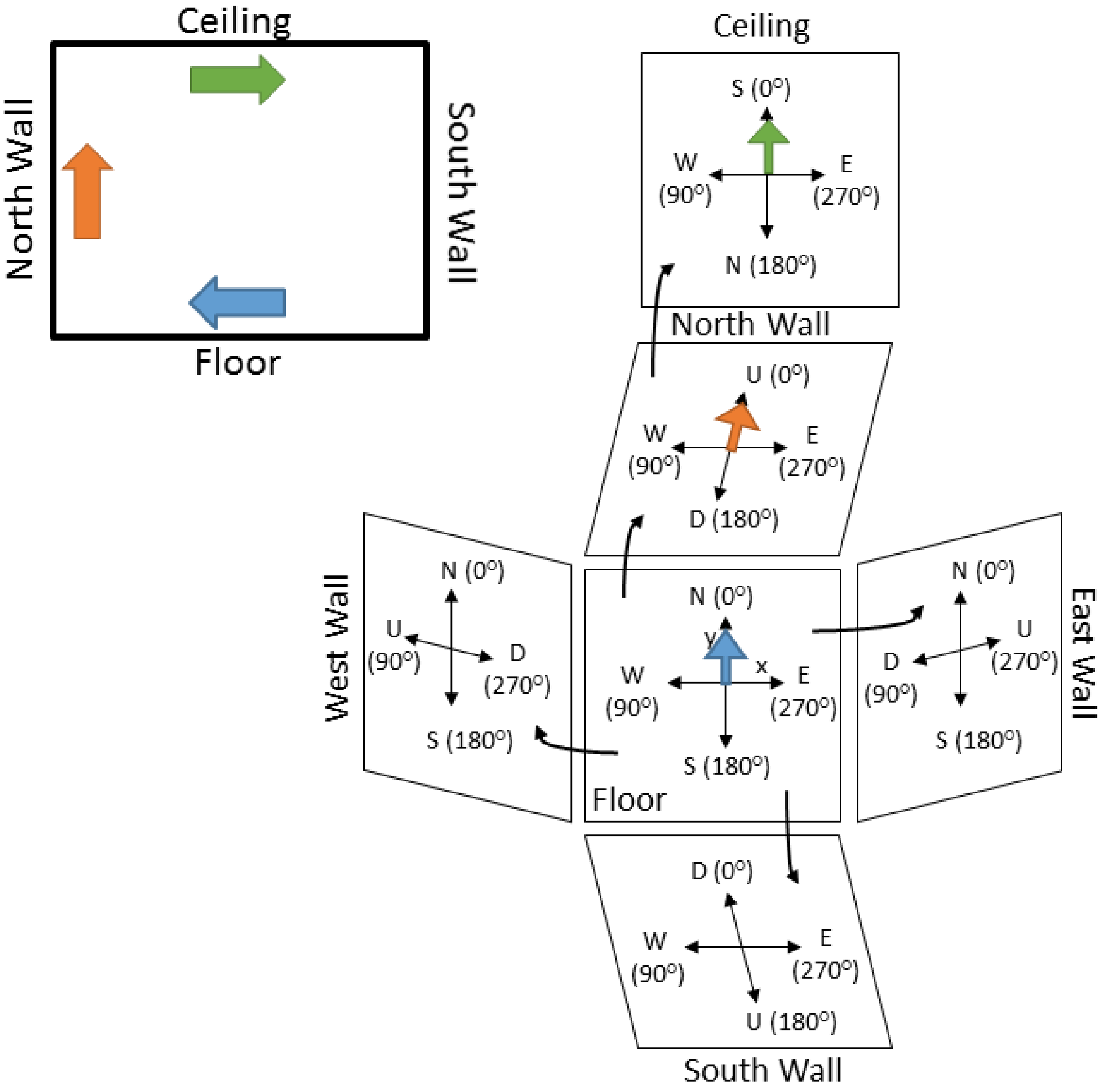

Figure 3.2. Coordinate system and reference frame in a 3D environment according to the extended-allocentric-heading hypothesis. The top left panel shows the lateral view. The right panel shows the unfold view of all six surfaces. The x-y coordinate system is shown on the room floor and as participants might rotate it by 90° as they locomote onto the vertical plane (i.e., the walls) or onto the inverted plane (i.e., the ceiling). The orientation of the coordinate system on each of the vertical walls is obtained by a 90° rotation of the coordinate system denoted on the floor. The orientation of the coordinate system on the ceiling is obtained by a 180° rotation of the

coordinate system denoted on the floor. The blue, orange and green arrows in sequence show the facing directions along a traversed route from the horizontal floor facing north to the vertical north wall facing up via a 90° pitch rotation, and to the inverted ceiling facing south via a 90° pitch rotation.

Can the extension hypothesis be applied to humans' head direction system? Humans are surface-based animals like rats. Furthermore, humans can use the coordinate system on the vertical wall in localization tasks (see Chapter 2) and can clearly distinguish horizontal and vertical movements even in a virtual reality environment where only visual stimuli are available to show the movements (Indovina et al., 2016). When the orientation of a map presented on a vertical wall was aligned with the perspective of viewing the horizontal path in the environment by a simple lay-down (90° forward rotation) transformation, judging the directions between points along the path was easier than judging the misaligned condition (Levine, Jankovic, & Palij, 1982). This suggests that at least in some circumstances like using a map, humans treat gravity up on the wall as equivalent to the front of their body and therefore extend a horizontal coordinate system to the vertical wall.

However, some other evidence suggests that humans may not have a toroidal coordinate system like bats. Using pitch rotation to extend individuals' allocentric heading on the floor to vertical walls and further on the ceiling might rely on locomotion experiences. Some neuroscience studies showed that rats have head direction cells in certain brain regions that can show changes responding to pitch rotations (Page et al., 2018; Stackman & Taube, 1998; Wilson, Page, & Jeffery, 2016). When the rats locomoted on the ceiling, which required a 180° pitch rotation, the head direction cells showed a dramatic change in activity (Calton & Taube, 2005).

These studies suggest that surface-based animals may not show a full toroidal coordinate system like bats in all 360° pitch rotations. It might be due to the fact that surface-based animals have usually had rare experiences to pitch more than 90° in their evolutionary and individual histories. For most humans, walking on vertical surfaces is very rare although sometimes we may walk on sloped surfaces with small inclines. Hence, the rare experiences of pitching our body 90° or more might prevent humans from spontaneously extending the allocentric heading on the ground to vertical and inverted surfaces.

Considering these factors, we propose two hypotheses alternative to the extended-allocentric-heading hypothesis. The first possibility is that people might ignore the yaw rotation on the ground before they locomote to other surfaces and would take their facing direction (e.g., north) as their heading. According to this hypothesis, people would treat the direction *up* of the opposite walls as the same heading although they locomote onto the two walls with two opposite allocentric headings on the ground. For example, people locomote onto the north wall with the heading of north on the ground and onto the south wall with the heading of south. In this case, people would use their facing direction as their heading regardless of the yaw rotation on the ground before they locomote to different vertical walls. When standing on the ceiling, people would also treat the direction *north* as the same heading as the direction *north* when standing on the ground although their facing direction of north standing on the ceiling is from a 180° pitch rotation of the facing direction of *south* on the ground. This hypothesis is very plausible. As we discussed above, while an upright person locomotes on the horizontal plane, the allocentric facing direction and allocentric heading are identical. This predominant experience in evolutional and individual history might shape human neural and cognitive mechanisms for spatial updating of their heading. Therefore, humans might always use their allocentric facing direction as their allocentric heading even when they stand upside-down by pitching 180º. We refer to this possibility as the allocentric-facing-direction hypothesis.

The second alternative hypothesis is that people might just use some preferred direction on the ground as their heading on the vertical or inverted surfaces regardless of the allocentric directions they are facing. This hypothesis assumes that participants might not be sensitive to either locomotion cues or environment cues to establish their headings on walls or ceilings. Therefore, they just establish their headings by retrieving the preferred reference direction used to learn object arrays on the ground. As shown in previous research, the preferred reference direction could be participants' initial facing direction, their last facing direction, or other salient reference directions due to environmental and layout characteristics on the ground (Kelly & McNamara, 2008; Mou & McNamara, 2002; Shelton & Marchette, 2010; Shelton & McNamara, 2001). According to this hypothesis, people would treat the direction *up* of the opposite walls as the same heading which could be their preferred direction on the ground. Similarly, when standing on the ceiling, people would treat the direction *north* or *south* as the same heading regardless of whether they actually face north or south. We refer to this possibility as the fixed-heading hypothesis.

Table 3.1. *Our three hypotheses and the corresponding predictions for the placement and JRD tasks.*

	Placement task			
	Wall		**Ceiling**	
	Up on the north wall	Up on the south wall	North on the ceiling	South on the ceiling
Extended-allocentric-heading hypothesis	North on the ground	South on the ground	South on the ground	North on the ground
Allocentric-facing-direction hypothesis	The same reference direction on the ground		North on the ground	South on the ground
Fixed-heading hypothesis	The same preferred direction on the ground		The same preferred direction on the ground	

	JRD task			
	Wall		**Ceiling**	
	Imagining North	Imagining South	Imagining North	Imagining South
Extended-allocentric-heading hypothesis	Easier when on the north wall	Easier when on the south wall	Easier when facing south	Easier when facing north
Allocentric-facing-direction hypothesis	No difference	No difference	No difference	No difference
Fixed-heading hypothesis	No difference	No difference	No difference	No difference

Note: The top rows of the table show the predictions on the placement task according to each of the three hypotheses, which are specified in the correspondence between Up on the north/south wall and the directions on the ground and between North/South on the ceiling and the directions on the ground. The bottom rows of the table show the predictions on the JRD task according to each of the three hypotheses, which are specified in the comparisons between the conditions when the participant was on the north/south wall or when the participant was facing north/south on the ceiling.

The current study tested the three hypotheses (see Table 3.1). To distinguish among these hypotheses, especially between the extended-allocentric-heading hypothesis and the allocentric-facing-direction hypothesis, is theoretically significant. The extended-allocentric-heading hypothesis is in line with the idea of locomotion-specific but species-universal. As long as individuals locomote onto walls or ceilings by pitch rotations, they will extend their 3D heading regardless of what species they belong to. By contrast, the allocentric-facing-direction hypothesis is more in line with the idea of species-specific. Different species locomote in environments in different ways. Some animals (e.g., bats) pitch and yaw whereas others species (e.g., humans) primarily yaw on the ground. Therefore, different neural and cognitive mechanisms are developed to accommodate their natural locomotion styles. In particular, humans locomote upright and yaw to change their heading. Therefore, they may treat their facing direction the same as their heading even when they stand on the ceiling upside-down via a pitch of 180º.

In the current study, participants learned an object array on the floor in a rectangular room with environmental cues. Later they navigated to a wall or the ceiling of the room via pitch rotations. According to the extended-allocentric-heading hypothesis (Figure 3.2), participants can extend their allocentric heading on the ground to walls and ceiling by pitch rotation when they locomote to those surfaces. Therefore, they would a) treat facing gravity Up on the north/south walls as an extended allocentric heading of north/south on the ground before the pitch rotation of 90° and b) treat facing North on the ceiling as the allocentric heading of South on the ground, and treat facing South on the ceiling as the allocentric heading of North on the ground before the pitch rotation of 180°. According to the allocentric-facing-direction hypothesis, participants do not encode their 3D allocentric headings but only encode the 3D allocentric directions. They use their allocentric facing direction to establish their 2D heading on the testing plane (walls or the ceiling). Therefore, participants would not differentiate between headings of facing gravity Up on the north/south walls and between headings of facing North on the ceiling and floor. However, they would differentiate between the headings of facing North and South on the ceiling. According to the fixed-heading hypothesis, participants neither encode their 3D allocentric headings nor use the 3D allocentric directions. They just establish their 2D heading on the plane (e.g., walls or the ceiling) by retrieving the preferred heading on the floor. Therefore, participants would not differentiate between headings of facing gravity Up on the north/south walls and between headings of facing North on the ceiling and floor. Furthermore, they would not differentiate between the headings of facing North and South on the ceiling.

We examined these three hypotheses by using two tasks. One task was to reconstruct the object array on the wall or on the ceiling after pitch rotations from the ground to the testing plane. Using the responses on the testing plane, we calculated the relationship between the directions on the testing plane (i.e., Up, North/South) and those on the ground (i.e., North). We assume that these relations between directions on the testing plane and on the ground reflect the relations between participants' allocentric headings when facing these directions on the testing plane and on the ground. Using these relations, we can test these three hypotheses (see more details about this method in Experiment 1).

The other task was a judgement of relative direction (JRD) task using the memories of the layout (for the paradigm, see Waller et al. (2002) for example). Participants were asked to imagine north or south directions on the ground and then make judgements about other directions on the ground. JRD tasks require participants to use 3D headings rather than 2D headings. For example, while both facing north and being asked to point to the east, an upright person should point to the right but an upside-down person should point to the left. Participants then should restore their 3D heading on the ground (upright and facing north or south) in the JRD task when they are physically standing on the walls or the ceiling. According to the extension hypothesis, participants have 3D headings (i.e., extended allocentric heading on the ground by a pitch rotation). This would allow them to restore their 3D heading on the ground by a mental pitch rotation in the reversed way. If the restored heading is aligned with the imagined heading, they can point to the target. If the restored heading is misaligned with the imagined heading, they need to mentally yaw the restored heading to make it align with the imagined heading. Therefore, the extended-allocentric-heading hypothesis would predict a *sensorimotor alignment effect*; i.e., the performance would be better when the imagined heading was the same as the extended allocentric heading during retrieval (Kelly, Avraamides, & Loomis, 2007; Mou, McNamara, Valiquette, & Rump, 2004; Shelton & Marchette, 2010). For example, for the imagined heading of North on the ground, facing South on the ceiling was easier than facing North on the ceiling. Because a typical sensorimotor alignment effect predicts that for the imagined heading of North on the ground, facing North on the ground is easier than facing South on the ground (as yaw is required in the latter to align the physical facing and the imagined heading), the *sensorimotor alignment effect* would appear in the opposite direction when people are standing on the ceiling. In contrast, as neither of the other two hypotheses claim that participants represent the 3D headings (the extended allocentric heading on the ground with the pitch rotation), they do not encode the transformation relations between their physical heading and imagined heading. As a consequence, participants might act as if they were tested in a remote room, not relevant to the learning room (Shelton & Marchette, 2010). Thus, they would not show any sensorimotor alignment effect. The predictions according to the three hypotheses are summarized in Table 3.1.

There were five experiment in the current study. In Experiments 1 and 2, we examined the allocentric heading updating from the ground to the vertical walls using the placement task and the JRD task, respectively. In Experiments 3 and 4, we examined the allocentric heading updating from the ground to the ceiling using the placement task and both tasks, respectively. Experiment 5 was a control experiment which examined the allocentric heading updating on a horizontal plane in a JRD task.

3.3 Experiment 1

3.3.1 Method

3.3.1.1 Participants. 64 university students participated in the experiment (age range = 17–37 years, *M* = 18.89 years, 32 females).

3.3.1.2 Apparatus. The experiment was conducted in a 4 × 4 m physical room. Participants saw the virtual experimental environments presented by an immersive virtual reality system that used Vizard software (WorldViz, Santa Barbara, CA), a head-mounted display (HMD, Oculus Rift, Oculus VR, LLC., Irvine, CA), and an InterSense-900 motion tracking system (InterSense, Inc., Billerica, MA). Screen resolution within the display was 2160 × 1200 pixels. The diagonal field of view (FOV) was 110°. Participants' physical viewing orientation was tracked by the IS-900 motion-tracking system so that they could physically rotate their bodies to change their viewing orientations in the virtual environment.

A joystick (Logitech ATK3, Logitech, Newark, CA) was used for translation in the virtual environment. The travel direction was determined by the projection of the direction of participants' viewing orientation onto the current travelling plane. When participants were on the corner of the two planes, they could move to the plane that they were looking at by pushing the joystick.

To make a pointing response, participants pointed a virtual wand at locations by controlling a physical pointer that was tracked by the InterSense motion tracking system. Participants could move the wand to indicate the response location and click a button on the wand to confirm the response.

3.3.1.3 Environment. The virtual experimental environment was a rectangular virtual room (Figure 3.3A). The room's size was 4 m wide, 8 m long, and 4 m high. The walls were homogeneously green with textures to increase the perceived optic flow during navigation. For simplicity, in rest of this paper, we use north, south, east and west to distinguish the directions on the ground. During the experiment, participants were never instructed with these terms. At each corner, to serve as feature / landmark cues, furniture was presented: a door, a bookshelf, a table, and a picture. The ceiling was light grey with a pattern of square textiles. Two lights were presented on the ceiling.

3.3.1.4 Materials and design. In the learning phase, a light grey round mat (2 m in diameter, 0.1 m in height) was presented at the center of the room on the ground to show the seven target objects (Figure 3.3B). The objects were a clock, a phone, a paperclip, a bottle, a lock, a candle, and a piece of wood. The association between the locations and objects was randomized across participants. A small blue platform (0.5 m in diameter, 0.1 m in height) was presented at the southwest side of the mat and 45° away from the orthogonal south to guide participants to locomote to the pre-determined learning position. In the testing phase, the mat and the platform (without objects) were displaced to the testing walls. The mat was presented at the center of the testing wall. The platform was presented at the left of the mat on the testing wall. Participants needed to navigate to the platform and then replace objects to the platform based on their memory of the objects' locations.

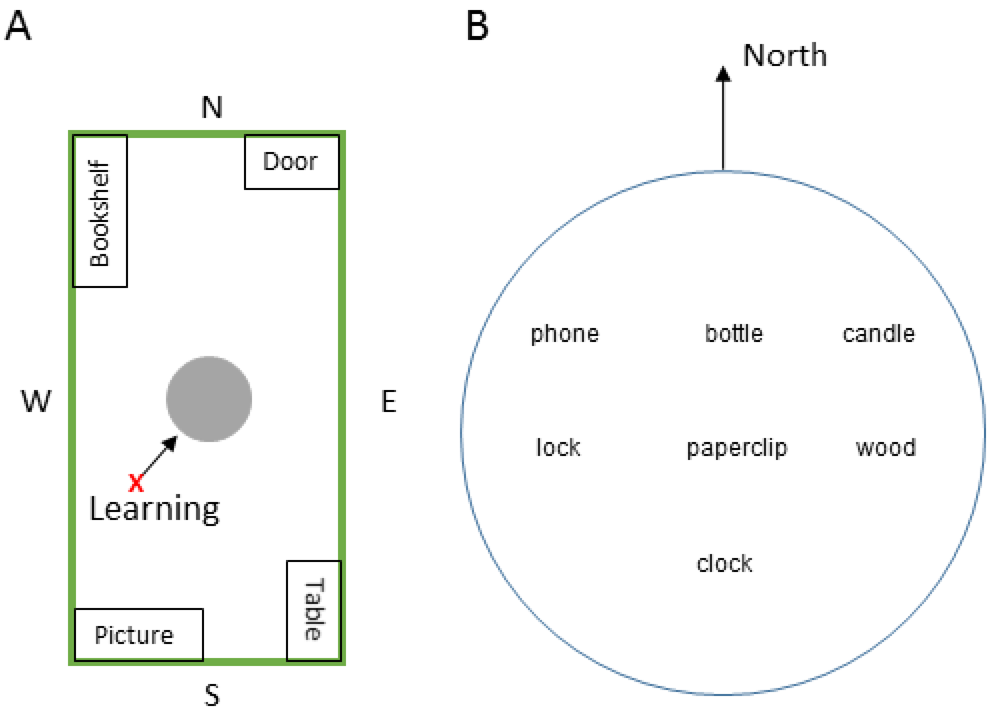

Figure 3.3. (A) Top view of the experimental environment. The arrow denotes the viewing direction in the learning phase. The X denotes the learning position. (B) An example of the object array. The main axis of the array was always oriented towards North on the ground. Object locations were the same across participants. For simplicity, object names are used to show the locations. For each participant, the objects were randomly assigned to the locations on the mat.

The primary independent variable is the testing wall (north or south). All participants navigated to both walls and replaced objects there. The order of the testing wall was randomized.

In addition, there were two groups of participants: upright and rotation. The only difference between the two groups was the navigation mode. The upright group always maintained an upright perspective, regardless of whether they were on the ground, the wall or the ceiling. When they reached a vertical wall, they climbed up along the wall, maintaining their perspective upright. The rotation group maintained an upright perspective when navigating on the ground. However, whenever they reached the boundary between two planes (e.g., the ground and the wall, or the wall and the ceiling), their perspective was rotated 90° upward (pitch up; see supplementary material for a rotation video). For example, when they reached a wall, their perspective was rotated 90° (pitch up) as if they were stepping on the wall and their body was perpendicular to the wall. When they navigated from the wall to the ground, their perspective was also rotated 90° (pitch up) so that they could return to an upright perspective when navigating on the ground.

The upright group actually had no pitch rotations and was designed as a baseline group to be compared with the rotation group, which actually had pitch rotation. Since both groups did the same task, the comparisons between the groups would indicate a) whether participants more likely extended their allocentric headings with actual pitch rotation than with mental pitch rotation and b) whether our manipulation of displaying pitch rotation in the virtual environment was effective. The participants were assigned equally into two groups (upright and rotation) with an equal number in each gender.

We also added a ground test phase after participants learned the layout of objects and before they navigated to the walls. In the ground test phase, participants navigated to a location east of the mat and then replaced the objects. The ground test was used to ensure that participants could update their allocentric heading when locomoting on the ground.

3.3.1.5 Procedure. Participants were tested individually. They were led into the experiment room blindfolded. First, they were introduced to the feature cues in the virtual environment and were asked to point to them with the wand. Then they practiced using the joystick to navigate in the environment, including locomoting on the north and south walls along the gravity up-down and the east-west axes. After that, they entered the formal experiment.

In the learning phase, the participants navigated to the platform and faced the mat, and stayed in this position during the entire learning phase. Therefore, the learning perspective was northeast. Before being presented with the objects, the participants once again pointed to the feature cues in the environment. Then the participants were asked to learn the array of seven target objects presented on the mat (Figure 3.3B). There were two learning blocks. In each block, the object array was presented for one minute and was removed. The participants used the wand to place the objects, which were probed at the bottom of the HMD screen sequentially in a random order. Their response locations were recorded. After the participants replaced all of the objects, the replaced objects were removed.

In the ground test phase, the participants navigated to the platform that had been displaced to the east of the mat, facing the mat (that is, facing west), and replaced the objects with the wand. Their response locations were recorded. There was no feedback regarding the accuracy of their placement. After all of the objects were placed, the replaced objects and the mat were removed.

In the wall test phase, the participants climbed up to each testing wall from the ground and navigated to the platform, and then replaced the objects on the mat. There was no feedback regarding the placement. The participants navigated back to the ground after the first wall test.

3.3.1.6 Calculation of estimated heading (H'). We calculated the participants' allocentric heading on the testing wall relative to North on the ground using the least square of angular discrepancy. For the sake of composition, we calculated the allocentric heading as if the participants were facing the direction of gravity Up. For every two objects (A and B, see Figure

3.4) of the learned layout, we calculated the bearing between the replaced locations of those objects on the testing wall (A' and B') relative to the direction of Up on the testing wall. Since there were seven objects, there were 21 possible pairs of objects, which makes 21 estimated bearings in total. Similarly, we calculated the bearing between the correct locations of the objects on the ground relative to any possible reference direction on the ground (we refer to this bearing as the correct bearing). For each corresponding pair of objects (e.g., A and B), we calculated the bearing error, which is the difference between the response bearing (the bearing of A'B' relative to the Up of the testing wall) and the correct bearing (the bearing of AB relative to the hypothetical reference direction on the ground). The hypothetical reference direction that leads to the least square of the bearing error across all 21 bearings is defined as the allocentric heading of Up on the testing wall relative to North on the ground. We refer to this estimated heading as H'. If participants treated the heading of facing Up as North on the floor, H' would be close to North according to this method.

To confirm the validity of this method, we also calculated the allocentric heading using participants' responses in the learning phase and ground testing phase. For the sake of composition, H' for the learning phase and ground testing phase was presented as if participants were facing North. In particular, we calculated the bearing between the replaced locations of any two objects (A' and B') relative to the direction of north rather than participants' physical facing direction. If this method works well, H' during the learning phase and ground testing phase should be very close to North. In addition, the finding that H' corresponding to the facing direction of North in the ground testing phase was closed to North would also support that participants updated their allocentric heading while navigating on the ground. To specify H', we use North as the direction of 0°.

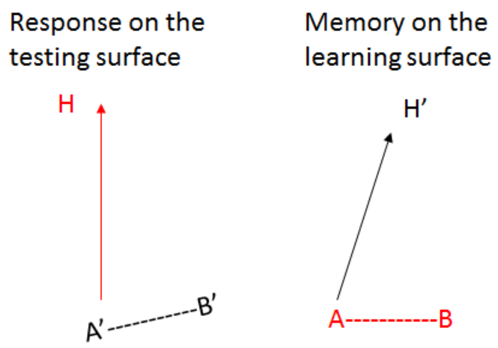

Figure 3.4. Correspondence between the estimated heading and the actual direction. A and B denote the actual positions of two objects. A’ and B’ denote the response positions of the two objects. H denotes an allocentric heading on the testing plane (e.g., in Experiment 1, Up on the wall). H’ denotes the estimated heading corresponding to H (e.g., in Experiment 1, North on the ground). The vector A’B’ relative to H is equal to the vector AB relative to H’.

3.3.2 Results and discussion

We calculated the estimated heading (H’) as described above for each participant and for the responses in each phase. Representative responses are plotted in Figures S1 and S2.

The H’s are plotted in Figures 3.5 and 3.6 for the two groups of upright and rotation, respectively, with the circular mean and 95% confidential intervals. For both groups, in the learning phases and the ground test, the H’ was around 0° (i.e., North on the ground) indicating that the participants successfully reconstructed the object array relative to the allocentric reference directions (e.g., North) from their learning perspective and from the new perspective in the ground testing phase. These results also indicated that the methods of calculating H’ are valid and participants updated their allocentric heading when navigating to the viewing position of the ground test.

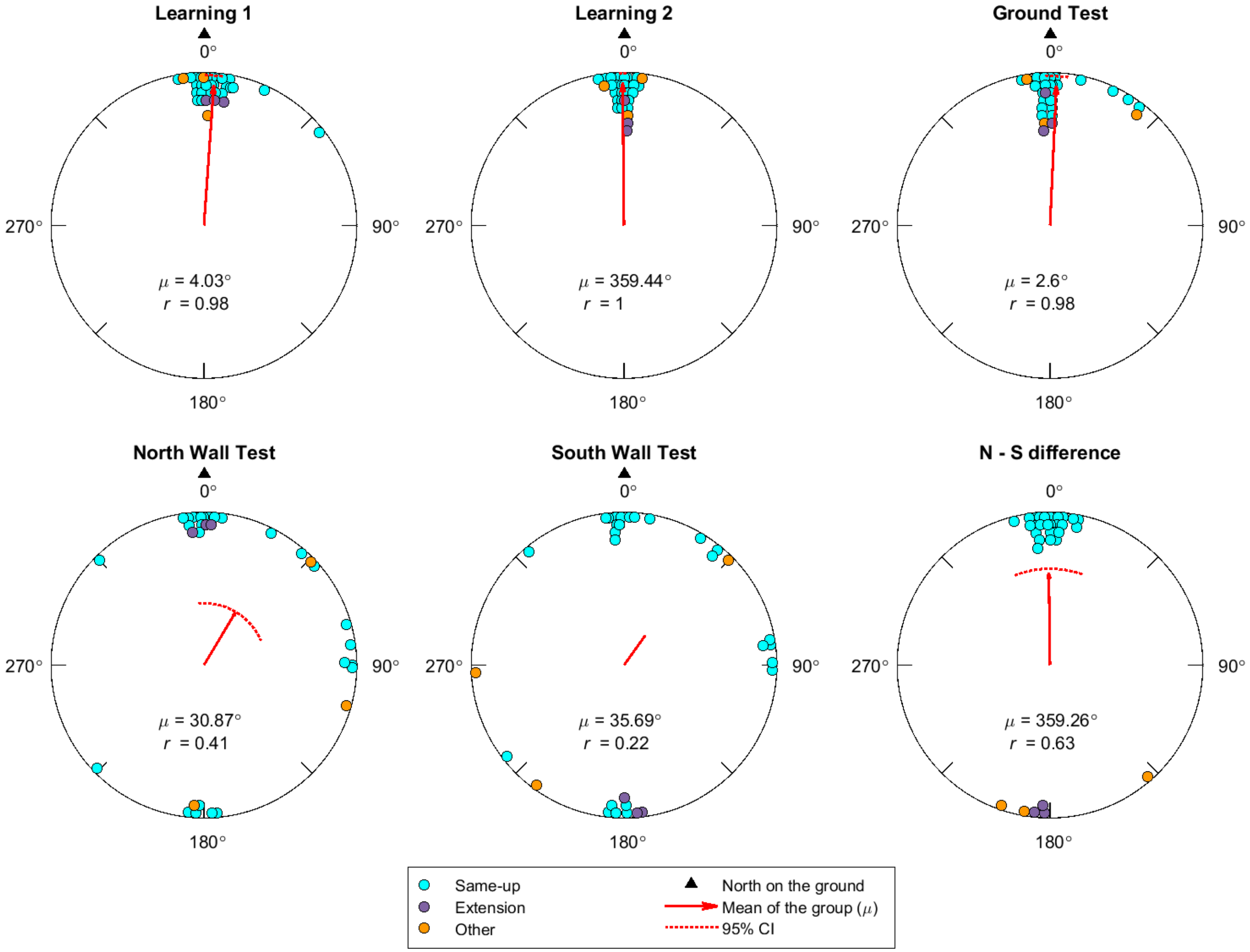
Learning 1
0°
90°
180°
270°
μ = 4.03°
r = 0.98
Learning 2
0°
90°
180°
270°
μ = 359.44°
r = 1
Ground Test
0°
90°
180°
270°
μ = 2.6°
r = 0.98
North Wall Test
0°
90°
180°
270°
μ = 30.87°
r = 0.41
South Wall Test
0°
90°
180°
270°
μ = 35.69°
r = 0.22
N - S difference
0°
90°
180°
270°
μ = 359.26°
r = 0.63
● Same-up
● Extension
● Other
▲ North on the ground
→ Mean of the group (μ)
95% CI

Figure 3.5. Estimated heading (H’) and angular difference in the upright group in Experiment 1 (placement task on the wall). Each dot indicates the H’ for one participant. The cyan dots represent the participants in the “same-up” category. The purple dots represent the participants in the “extension” category. The orange dots represent the participants in the “other” category. The black triangle indicates North on the ground (0°). The red arrow indicates the circular direction (*μ*) and the length (*r*) of the mean vector of the H’ across all participants. The arc above the mean direction indicates the 95% confidence interval of the mean direction.

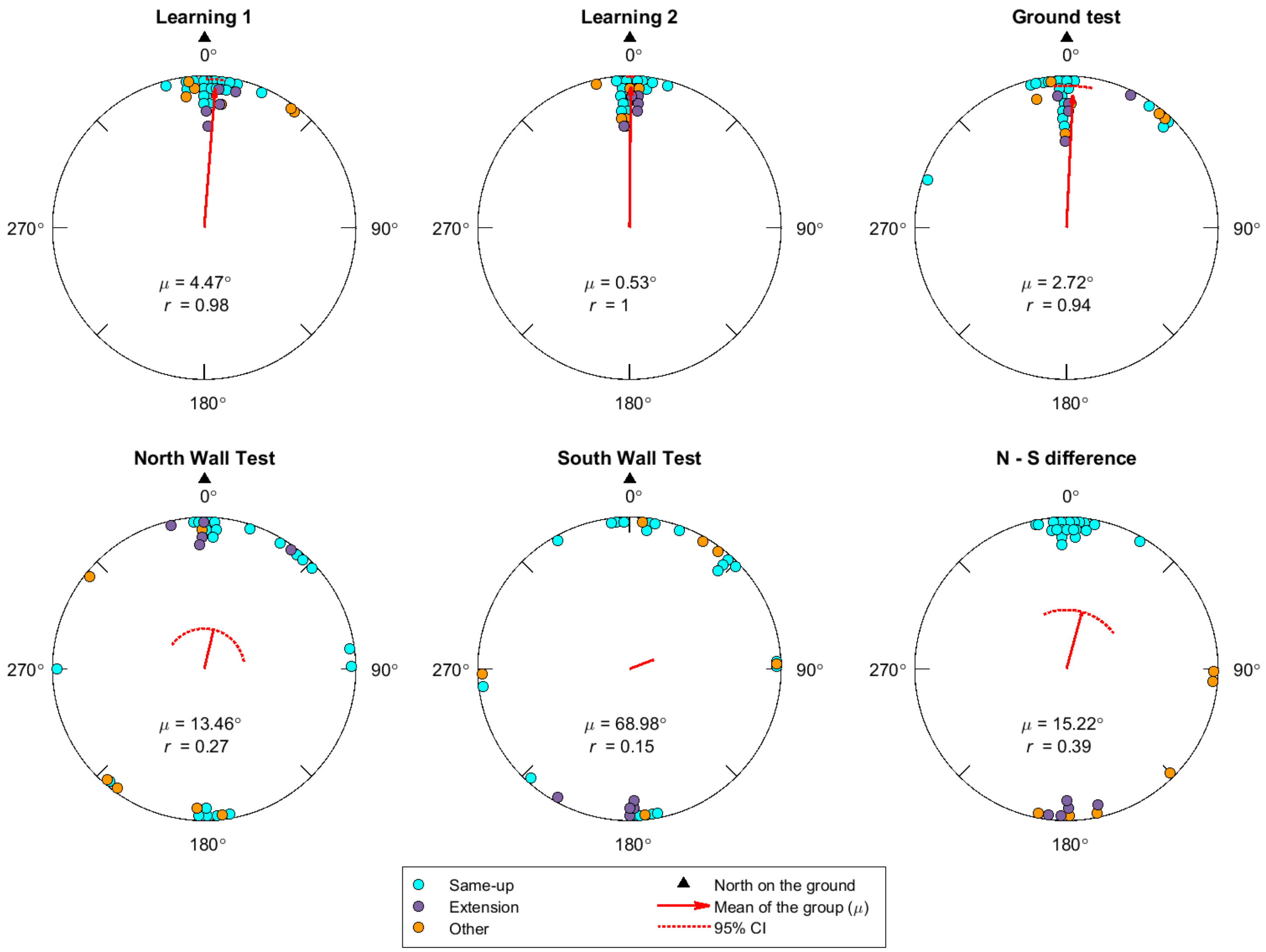
Learning 1
0°
90°
180°
270°
μ = 4.47°
r = 0.98
Learning 2
0°
90°
180°
270°
μ = 0.53°
r = 1
Ground test
0°
90°
180°
270°
μ = 2.72°
r = 0.94
North Wall Test
0°
90°
180°
270°
μ = 13.46°
r = 0.27
South Wall Test
0°
90°
180°
270°
μ = 68.98°
r = 0.15
N - S difference
0°
90°
180°
270°
μ = 15.22°
r = 0.39
Same-up
Extension
Other
North on the ground
Mean of the group (μ)
95% CI

Figure 3.6. Estimated heading (H') and angular difference in the rotation group in Experiment 1 (placement task on the wall). Each dot indicates the H' for one participant. The cyan dots represent the participants in the "same-up" category. The purple dots represent the participants in the "extension" category. The orange dots represent the participants in the "other" category. The black triangle indicates North on the ground (0°). The red arrow indicates the circular direction (μ) and the length (r) of the mean vector of the H' across all participants. The arc above the mean direction indicates the 95% confidence interval of the mean direction.

Rayleigh tests were conducted for each wall test. The results showed that for the upright group, in the south wall test, the H' were uniformly distributed ($Z = 1.61$, $p = .201$) whereas in the north wall test, the H' were not ($Z = 5.26$, $p = .004$). For the rotation group, in both tests, the H' were uniformly distributed (north wall: $Z = 2.26$, $p = .104$; south wall: $Z = 0.72$, $p = .488$). These results suggest that for both groups, the H's in single wall tests were noisy. This result could have occured because participants had randomly replaced the object array on the testing walls. However, it is also possible that different participants might have selected the different reference directions using egocentric, allocentric, or intrinsic cues to encode the object array (e.g., Kelly & McNamara, 2008) but that each individual participant always mapped the Up on the testing wall to the reference direction in encoding the object array.

To test this possibility, we examined the angular difference between the H's in the north wall test and the south wall test for each participant. We also plotted the angular differences in Figures 3.5 and 3.6 (N-S difference) for these two groups. We found that for most of the participants, the angular difference between H's in the north and south wall tests was around 0° (angle range [0°, 45°] or [315°, 360°]) whereas for the rest, the angular difference was around

180° (angle range [135°, 225°]). Clearly, in both the upright and rotation groups, most of the participants had the same or similar H' in both wall tests. This type of response was found in 26 participants in the upright group (81.25%) and in 21 participants in the rotation group (65.63%). These participants considered Up on the north and south walls to be the same or a similar direction on the ground, which indicates that they did not have 3D extended allocentric heading (i.e., extended yaw with a rotation of pitch) on the testing planes. This contradicts the extended-allocentric-heading hypothesis. However, we could not determine whether the participants merely retrieved the encoded reference direction from memory (according to the fixed-heading hypothesis) or established a 2D heading using the allocentric reference directions (according to the allocentric-facing-direction hypothesis). These participants were categorized as "same-up" (see the blue dots in Figures 3.5 and 3.6). We also summarized the percentages of different categories in Table 3.2.

Several of the rest of the participants showed a pattern of extending their allocentric heading (see the purple dots in Figures 3.5 and 3.6) according to the extended-allocentric-heading hypothesis. Specifically, according to their replaced locations, Up on the north wall was close to North on the ground (i.e., H's were around 0°; angle range [0°, 45°] or [315°, 360°]) and Up on the south wall was close to South on the ground (i.e., H's were around 180°; angle range [135°, 225°]). This type of response was found in three participants in the upright group (9.38%) and in five participants in the rotation group (15.63%). These participants were categorized as "extension."

There were three participants in the upright group (9.38%) and six in the rotation group (18.75%) whose responses could not fit into any of the two categories. These participants were categorized as "other."

Comparing the numbers of participants with the three types of responses in the upright group with those in the rotation group, numerically the rotation group showed more participants in the “extension” category than the upright group although the Chi-square test did not show a significant difference [$\chi^2(2, n = 64) = 2.03, p = .362$].

In Experiment 1, we found that for both the upright and rotation groups, the majority of the participants (i.e., the participants in the “same-up” category) did not spontaneously extend their allocentric heading from the ground to the testing walls, which seems to violate the extended-allocentric-heading hypothesis. Instead, a relatively small portion of participants (i.e., those in the “extension” category) did extend their allocentric heading from the ground to the vertical walls.

Although our placement task showed that only a minority of participants extended their allocentric heading while moving from the ground to the wall, the “same-up” participants might also have been able to do that but they did not demonstrate that because the placement task might not have required them to do so. When participants replaced objects, they may have only associated the reference directions on the testing walls with the reference directions on the ground without considering their own headings.

Table 3.2. *Summary of the frequencies and percentages of different categories in the placement task.*

	Wall			
	Same-up	**Extension**	**Other**	**Total**
Experiment 1 Upright	26 (81.25%)	3 (9.38%)	3 (9.38%)	N = 32
Experiment 1 Rotation	21 (65.63%)	5 (15.63%)	6 (18.75%)	N = 32

	Ceiling				
	Fixed	**North is north**	**Extension**	**Other**	**Total**
Experiment 3 Upright	8 (25%)	17 (53.13%)	1 (3.13%)	6 (18.75%)	N = 32
Experiment 3 Rotation	20 (45.45%)	10 (22.73%)	8 (18.18%)	6 (13.64%)	N = 44
Experiment 4 Rotation	32 (40%)	22 (27.5%)	17 (21.25%)	9 (11.25%)	N = 80

Note: The top rows of the table show the results in Experiment 1. The bottom rows show the results in Experiments 3 and 4. The numbers in the parentheses show the percentage of the frequency out of the total number of participants in that group.

In Experiment 2, we used the judgement of relative direction (JRD) task to further examine whether participants could extend their allocentric heading when they locomoted from the floor to the walls. In particular, we examined whether there were sensorimotor alignment effects in JRD tasks when participants physically faced Up on the North/South walls and imagined facing North/South on the ground. As discussed in the Introduction, the judgement of relative direction (standing at A, facing B, point to C) tasks require participants to mentally adopt their 3D heading on the ground (i.e., standing upright and *yaw*ing according to the bearing from A to B). If participants extended their 3D heading on the testing wall, then they might have mentally pitched back to the ground. When the extended heading was the same as the imagined heading, they had already adopted the imagined heading on the ground. When the extended heading was not the same as the imagined heading, they needed to yaw to further adopt the imagined heading. Therefore, compared with physically facing Up on the south wall, physically facing Up on the north wall would facilitate the imagined heading of North on the ground. In contrast, neither the allocentric-facing-direction hypothesis nor the fixed-heading hypothesis stipulate that participants had 3D allocentric heading on the testing wall; thus, participants might merely retrieve their memory of the layout of the object as if they were standing in a remote room. Therefore, according to these two hypotheses, there would be no sensorimotor alignment effect (see Table 3.1).

3.4 Experiment 2

3.4.1 Method

3.4.1.1 Participants. 32 university students participated in the experiment (age range = 17–28 years, *M* = 19.59 years) with an equal number in each gender.

3.4.1.2 Apparatus and environment. The apparatuses were exactly the same as in Experiment 1 with the following exceptions. First, to translate in the virtual environment, the participants pushed the forward button of a wireless controller (Oculus Touch, Oculus VR, LLC., Irvine, CA). Second, the joystick (Logitech ATK3, Logitech, Newark, CA) was used for making a response in the JRD task. The resolution of the joystick was 1°. The experimental environment was exactly the same as Experiment 1.

3.4.1.3 Materials and design. There are several differences between this experiment and Experiment 1. First, only the rotation group was used in Experiment 2, as using the upright or rotated perspective did not significantly affect the results in Experiment 1. Second, in the ground test phase, the platform was presented at either the north or the south of the mat on the ground. This position was counterbalanced between participants. Third, in the testing phase, the platform was presented at the middle bottom of the wall (0.8 m from the ground) and exactly below the mat. Therefore, participants faced Up standing at the platform during the testing phase. Last, the placement tests were replaced by the JRD test on each testing wall.

JRD tests consisted of 12 trials, six for imagining north and six for imagining south on the ground, presented in a randomized sequence (see Table 3.3). On each trial, the participants were presented the texts on the screen of the HMD: "*Imagine you are standing at Object A, facing Object B.*" Then they clicked a button on the joystick to see the text: "*point to Object C.*" Objects A, B, and C were from the object array in the learning phase as shown in Table 3.3. Object A was the imagined position. Object B was the imagined facing object. Object C was the target. The participants were asked to respond as quickly as possible without sacrificing accuracy. The response direction and the latencies for orientation and pointing response were recorded. There was no feedback for the responses.

3.4.1.4 Procedure. The procedure for Experiment 2 was exactly the same as for Experiment 1 with the following exceptions. Since in each trial of the JRD task, the names of objects were presented to the participants, the experimenter named each object in the first learning block.

Table 3.3. *Trial list in the JRD task in Experiment 2.*

Imagined heading on the ground	**Imagined position**	**Imagined facing object**	**Target object**
North	wood	candle	phone
North	clock	paperclip	lock
North	clock	paperclip	candle
North	wood	candle	clock
North	lock	phone	clock
North	lock	phone	paperclip
South	paperclip	clock	phone
South	phone	lock	paperclip
South	phone	lock	wood
South	paperclip	clock	candle
South	candle	wood	bottle
South	candle	wood	paperclip

Note: For simplicity, object names are used in the table to show the locations. See Figure 3.3B for the object locations. For each participant, the objects were randomly assigned to the locations on the mat.

3.4.2 Results and discussion

The mean and standard deviations of absolute pointing error and those of response latency are shown in Table 3.4. Response latency as a function of physical facing direction (North, South) and imagined heading direction (North, South) is plotted in Figure 3.7. The absolute pointing error showed the same general pattern as the angular error. There was no evidence of speed-accuracy trade-offs. For brevity, here we only report the results from the statistical tests using response latency as the dependent variable.

Table 3.4. *Mean and standard deviation for absolute pointing error and response latency in the JRD task in Experiment 2.*

Wall	**Imagined direction**	**Absolute pointing error (°)**	**Response latency (seconds)**
		Mean (*SD*)	*Mean* (*SD*)
North	North	37 (17.17)	4.98 (4.16)
North	South	38 (24.01)	5.02 (3.08)
South	North	33 (19.76)	5.39 (5.03)
South	South	33 (18.30)	5.41 (3.13)

A 2 × 2 repeated-measure ANOVA (Physical Position [North wall, South wall] × Imagined Heading Direction [North, South]) was conducted. There was no significance in the main effects, or the interaction (*p*s > .24, partial $\eta^2 < .05$).

We did not find the sensorimotor alignment effect in this experiment. This result is consistent with what we found in Experiment 1. According to the results in Experiment 1, the majority of participants did not establish their 3D allocentric heading by extending their allocentric heading (yaw rotation) on the ground with pitch rotation when they navigated to the wall from the ground. As sensorimotor alignment effects rely on the transformation relations between the 3D heading on the testing walls and the imagined 3D heading on the ground, no sensorimotor effect would be expected if the majority of participants did not encode or extend the 3D heading on the testing walls. The consistency between the results of Experiments 1 and 2 further verified that the placement task could indicate the participants' allocentric heading representation.

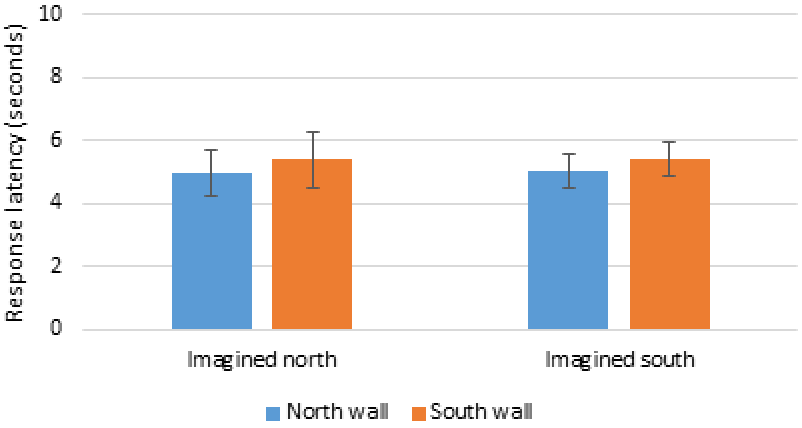

Figure 3.7. Response latency in Experiment 2 (JRD task on the wall). Error bars represent standard errors of the mean.

3.5 Experiment 3

The primary purpose of Experiment 3 was to further test the three hypotheses by examining the participants' allocentric heading when they navigated from the ground to an inverted horizontal plane (i.e., ceiling). Participants navigated to the ceiling via the walls (north or south) and then replaced objects on the ceiling from two opposite facing directions (South or North). The extended-allocentric-heading hypothesis predicts that participants would have a heading of North (or South) when they face South (or North) on the ceiling by traversing over the north (or south) wall (Table 3.1). The allocentric-facing-direction hypothesis predicts that participants would establish their 2D heading using the allocentric reference directions. Thus, their headings would be north (or south) when they face north (or south). The fixed-heading hypothesis predicts that participants would merely retrieve their preferred heading encoded on the ground regardless of their facing direction. Thus they would have the same heading whether they faced North or South direction on the ceiling.

3.5.1 Method

3.5.1.1 Participants. 76 university students participated in the experiment (age range = 17–44 years, *M* = 19.05 years). The participants were assigned into two groups (upright and rotation). There were 32 participants in the upright group (16 females) and 44 in the rotation group (21 females).

3.5.1.2 Apparatus and environment. These were the same as in Experiment 1.

3.5.1.3 Materials and design. These were the same as Experiment 1 with the following exceptions. First, in the ground test phase, the platform was presented at either the north or the south of the mat on the ground (i.e., the same as in Experiment 2). Second, the wall placement tests were replaced by the ceiling tests. In each ceiling test, the mat was presented at the center of the ceiling. In the north test, in which participants traversed over the north wall, the platform was presented at the north to the mat. In the south test, the platform was presented at the south to the mat. Participants took both the north test and south test. The testing order was counterbalanced across participants.

3.5.1.4 Procedure. The procedure for Experiment 3 was the same as for Experiment 1 with the following exceptions. Before the formal experiment, participants practiced using the joystick to navigate on the walls horizontally and vertically, and also navigated on the ceiling. On each ceiling test, the participants climbed up to the ceiling via the wall closer to the platform and navigated to the platform, and then replaced the objects on the mat. There was no feedback for their placement. Between the two tests, the participants returned to the ground via the same wall and then went to the next testing position via the opposite wall.

3.5.2 Results and discussion

As in Experiment 1, for both the upright and rotation groups, we calculated the estimated heading (H') from the responses in each phase when the participants were facing a direction on the testing plane relative to North of the ground. In the learning and ground tests, the estimated heading still corresponded to the facing direction of North. Thus, estimated headings should have been closed to North as participants accurately encoded and updated their headings on the ground. In the ceiling tests, the estimated heading corresponded to the participants' actual facing direction. In particular, when participants faced South, we calculated the estimated heading of facing South. Thus, if participants extended their heading, then the estimated heading of facing South would be close to North on the ground (0°). If participants used the allocentric facing direction, then the estimated heading of facing South would be close to South on the ground (180°). If participants used the preferred heading regardless of the allocentric facing direction, then the estimated heading of facing South would be similar to that of facing North in the ceiling test (Table 3.1).

Representative responses are plotted in Figures S3, S4, and S5. The results were plotted in Figures 3.8 and 3.9 for the two groups, respectively, with the circular mean and 95%

confidential intervals for each phase. For both groups, in the learning phases and the ground test, the H’ were around 0° (i.e., North on the ground), which indicates that the participants successfully reconstructed the object array from the learning heading and updated their allocentric heading when moving to the testing perspective of the ground test.

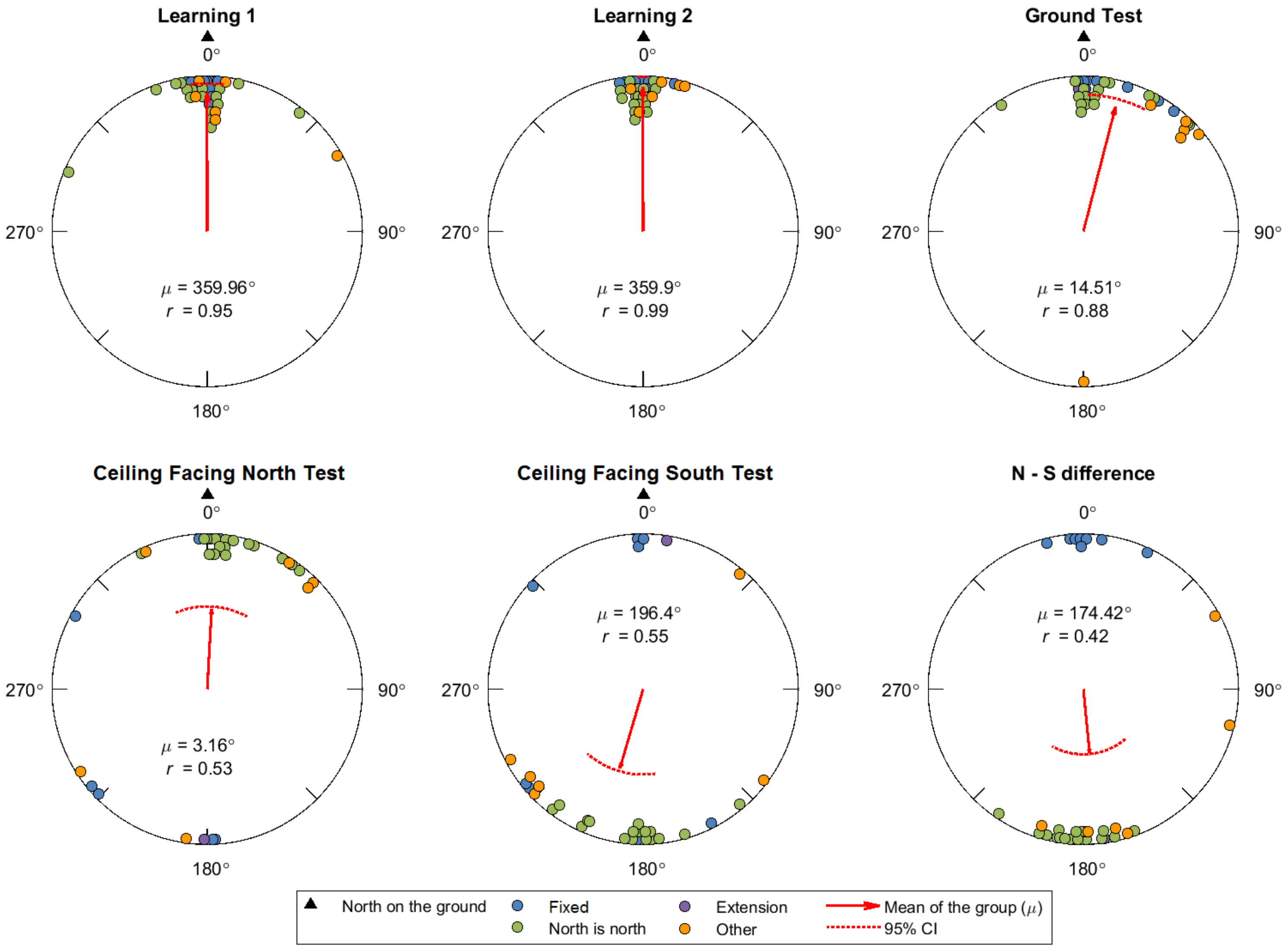
Learning 1
0°
90°
180°
270°
μ = 359.96°
r = 0.95
Learning 2
0°
90°
180°
270°
μ = 359.9°
r = 0.99
Ground Test
0°
90°
180°
270°
μ = 14.51°
r = 0.88
Ceiling Facing North Test
0°
90°
180°
270°
μ = 3.16°
r = 0.53
Ceiling Facing South Test
0°
90°
180°
270°
μ = 196.4°
r = 0.55
N - S difference
0°
90°
180°
270°
μ = 174.42°
r = 0.42
▲ North on the ground
● Fixed
● North is north
● Extension
● Other
Mean of the group (μ)
95% CI

Figure 3.8. Estimated heading (H') and angular difference in the upright group in Experiment 3 (placement task on the ceiling). Each dot indicates the H' for one participant. The blue dots represent the participants in the "fixed" category. The green dots represent the participants in the "north is north" category. The purple dots represent the participants in the "extension" category. The orange dots represent the participants in the "other" category. The black triangle indicates North on the ground (0°). The red arrow indicates the circular direction (μ) and the length (r) of the mean vector of the H' across all participants. The arc above the mean direction indicates the 95% confidence interval of the mean direction.

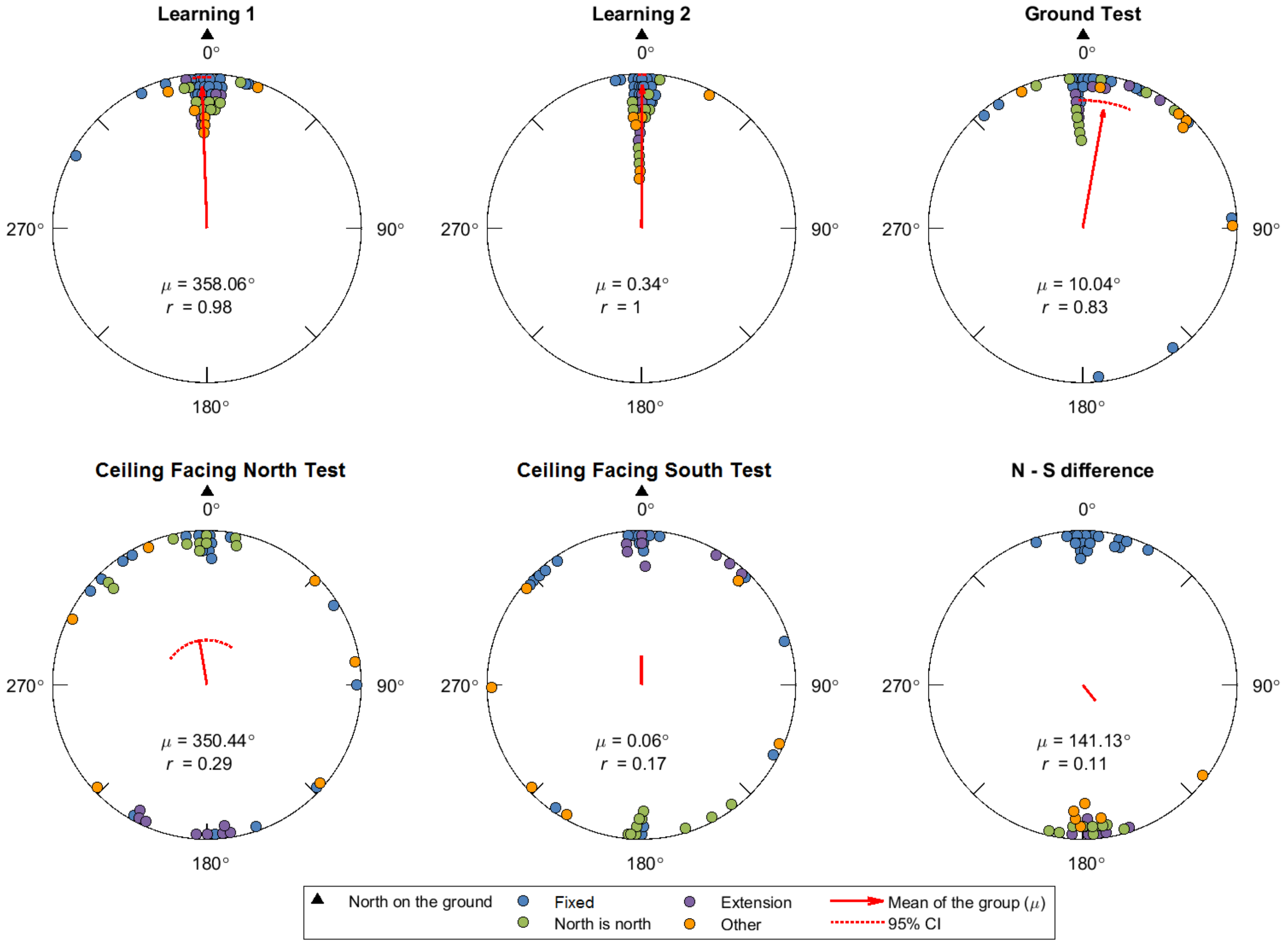
Learning 1
0°
90°
180°
270°
μ = 358.06°
r = 0.98
Learning 2
0°
90°
180°
270°
μ = 0.34°
r = 1
Ground Test
0°
90°
180°
270°
μ = 10.04°
r = 0.83
Ceiling Facing North Test
0°
90°
180°
270°
μ = 350.44°
r = 0.29
Ceiling Facing South Test
0°
90°
180°
270°
μ = 0.06°
r = 0.17
N - S difference
0°
90°
180°
270°
μ = 141.13°
r = 0.11
North on the ground
Fixed
North is north
Extension
Other
Mean of the group (μ)
95% CI

Figure 3.9. Estimated heading (H') and angular difference in the rotation group in Experiment 3 (placement task on the ceiling). Each dot indicates the H' for one participant. The blue dots represent the participants in the "fixed" category. The green dots represent the participants in the "north is north" category. The purple dots represent the participants in the "extension" category. The orange dots represent the participants in the "other" category. The black triangle indicates North on the ground (0°). The red arrow indicates the circular direction (μ) and the length (r) of the mean vector of the H' across all participants. The arc above the mean direction indicates the 95% confidence interval of the mean direction.

Rayleigh tests were conducted for each ceiling test. The results showed that for the upright group, in both tests, the H's were not uniformly distributed (ps < .001). For the rotation group, in the ceiling-facing-south test, the H's were uniformly distributed ($Z = 1.31$, $p = .271$) whereas in the ceiling facing north test, the H's were not ($Z = 3.72$, $p = .023$).

Again, we examined the angular difference between H's in the ceiling-facing-north test and the ceiling-facing-south test for each participant and then categorized participants who showed different types of responses. The results of the categorization are listed in Table 3.2.

In both the upright and rotation groups, we found that some participants had the same or similar H's in both tests (i.e., the angular differences were around 0°; angle range [0°, 45°] or [315°, 360°]). In other words, from the participants' egocentric view, their responses were basically the same, regardless of their actual facing direction. This type of response was found in eight participants in the upright group (25%) and 20 participants in the rotation group (45.45%). These participants did not use the environmental cues or their locomotion from the floor to the ceiling and instead likely just retrieved a fixed heading from their memories. They were categorized as “fixed” (see the blue dots in Figures 3.8 and 3.9).

For the rest of participants, we further categorized those who showed that the angular difference of H’ in the two ceiling tests was around 180° (angle range [135°, 225°]).

For some participants, their responses indicate that facing North on the ceiling equalled facing North on the ground (i.e., H’s were around 0°; angle range [0°, 45°] or [315°, 360°]) and facing South on the ceiling equalled facing South on the ground (i.e., H’s were around 180°; angle range [135°, 225°]). This type of response was found in 17 participants in the upright group (53.13%) and 10 participants in the rotation group (22.73%). We speculate that such participants in the rotation group used environmental cues to find reference directions (e.g., North) but they seemed to ignore their inverted perspective and the pitch rotations. Therefore the participants who showed this type of response were categorized as “north is north” (see the green dots in Figures 3.8 and 3.9).

The total percentage of the “fixed” and “north is north” categories together in Experiment 3 was similar to that of the “same-up” category in Experiment 1. We speculate that the “same-up” category in the wall tests included both the “fixed” and “north is north” categories. These two categories could not be distinguished from each other using the wall placement task in Experiment 1.

Some other participants’ responses indicate that facing North on the ceiling was equal to facing South on the ground (i.e., H’s were around 180°; angle range [135°, 225°]) and that facing South on the ceiling was equal to facing North on the ground (i.e., H’s were around 0°; angle range [0°, 45°] or [315°, 360°]). This type of response was found in one participant in the upright group (3.13%) and eight participants in the rotation group (18.18%). Such participants in the rotation group could have used the pitch rotation to extend their allocentric heading on the floor. Therefore the participants who showed this type of response were categorized as "extension" (see the purple dots in Figures 3.8 and 3.9).

Six participants in the upright group (18.75%) and six participants in the rotation group (13.64%) were categorized as "other"; i.e., those whose response could not fit into any of the three categories.

We compared the numbers of participants with the three types of responses in the upright group with those in the rotation group. A Chi-square test showed a significant difference [$\chi^2(3, n = 76) = 10.78, p = .013$]. Comparing the percentages of "extension" participants in the two groups, we found that there were more participants in the rotation group than in the upright group, which suggests that self-locomotion (physical pitch rotation) helped to extend the allocentric heading on the ground by a pitch rotation. In the wall conditions (Experiment 1), we did not find such a facilitation of pitch rotation on the extended heading. This discrepancy may have occurred because, first, mentally pitching 90° is easier than mentally pitching 180°; and second, participants could have had an experience of a pitch of 90° by looking up 90° but could hardly have had the experience of a pitch of 180° in their daily life. Thus the visual pitch rotation facilitated an extension of headings when the participants moved to the ceiling by a pitch of 180° but not when they moved to walls by a pitch of 90°.

Most important, consistent with the previous experiments, the results of Experiment 3 still indicate that most participants did not spontaneously extend their allocentric headings on the ground to other planes (only about 18% of participants in the rotation group did). To verify this conclusion based on the placement task in Experiment 3, Experiment 4 used both the placement and JRD tasks. Participants did JRD tasks on the ceiling by climbing over the north and south walls before they replaced the objects on the ceiling by climbing over the north and south walls again. We first used the placement task to categorize participants, and then used the JRD task to examine whether each category of participants could show any sensorimotor alignment effect. According to the extended-allocentric-heading hypothesis, the “extension” participants would show a reversed sensorimotor alignment effect. In particular, the performance would be better when the imagined heading (e.g., South) was the same as the extended allocentric heading but opposite to the facing direction (e.g., an extended heading of south when facing north on the ceiling) than when the imagined heading was opposite to the extended allocentric heading but the same as the facing direction (e.g., extended heading of north when facing south on the ceiling). For the other two groups ("fixed” and “north is north” participants), there would be no sensorimotor alignment effect because these two groups did not establish 3D allocentric headings according to the fixed-heading hypothesis and the allocentric-facing-direction hypothesis, and because sensorimotor alignment effects require 3D allocentric heading.

3.6 Experiment 4

3.6.1 Method

3.6.1.1 Participants. 80 university students participated in the experiment (age range = 17–60 years, *M* = 20.19 years) with an equal number in each gender. The sample size was about twice that of Experiment 3 because we intended to increase the number of participants in each category in order to examine the performance of each category in the JRD task.

3.6.1.2 Apparatus and environment. They were the same as Experiment 2.

3.6.1.3 Materials and design. They were the same as Experiment 3 except that the ceiling JRD tests were added before the placement task and only the rotation group was used. The JRD trials were the same as those used in Experiment 2.

3.6.1.4 Procedure. The procedure of Experiment 4 was the same as Experiment 3 except that the ceiling JRD tests were added before the ceiling placement tests. The JRD tests were conducted earlier than the placement tests to avoid having participants rely on the visual memories of their replaced layout on the ceiling in the JRD tests.

On each ceiling JRD test, the participants navigated to the platform at the north or south of the mat via the north or south walls and faced the mat at the center of the ceiling, and then did the JRD task. They were instructed not to rotate their head or body but always keep the same heading direction. After the JRD tests, participants did the placement task on the ceiling at the north and south of the mat (same as Experiment 3). Between the two JRD tests and between the two placement tests, the participants returned to the ground and then went to the opposite wall and then navigated to the next testing position. Participants alternately faced south or north across the four testing phases and their first facing direction of the four testing phases was counterbalanced across participants.

3.6.2 Results and discussion

As in Experiment 3, for the responses in each placement phase, we calculated the estimated heading (H’). The results were plotted in Figure 3.10 with the circular mean and 95% confidential intervals for each phase. In the learning phases and the ground test, the H’ was around 0° (i.e., North on the ground), which indicates that the participants successfully reconstructed the object array from their learning heading and updated their allocentric heading of facing the testing direction on the ground test. Rayleigh tests were conducted for each ceiling test. The results showed that in both tests, the H’s were not uniformly distributed ($ps < .007$).

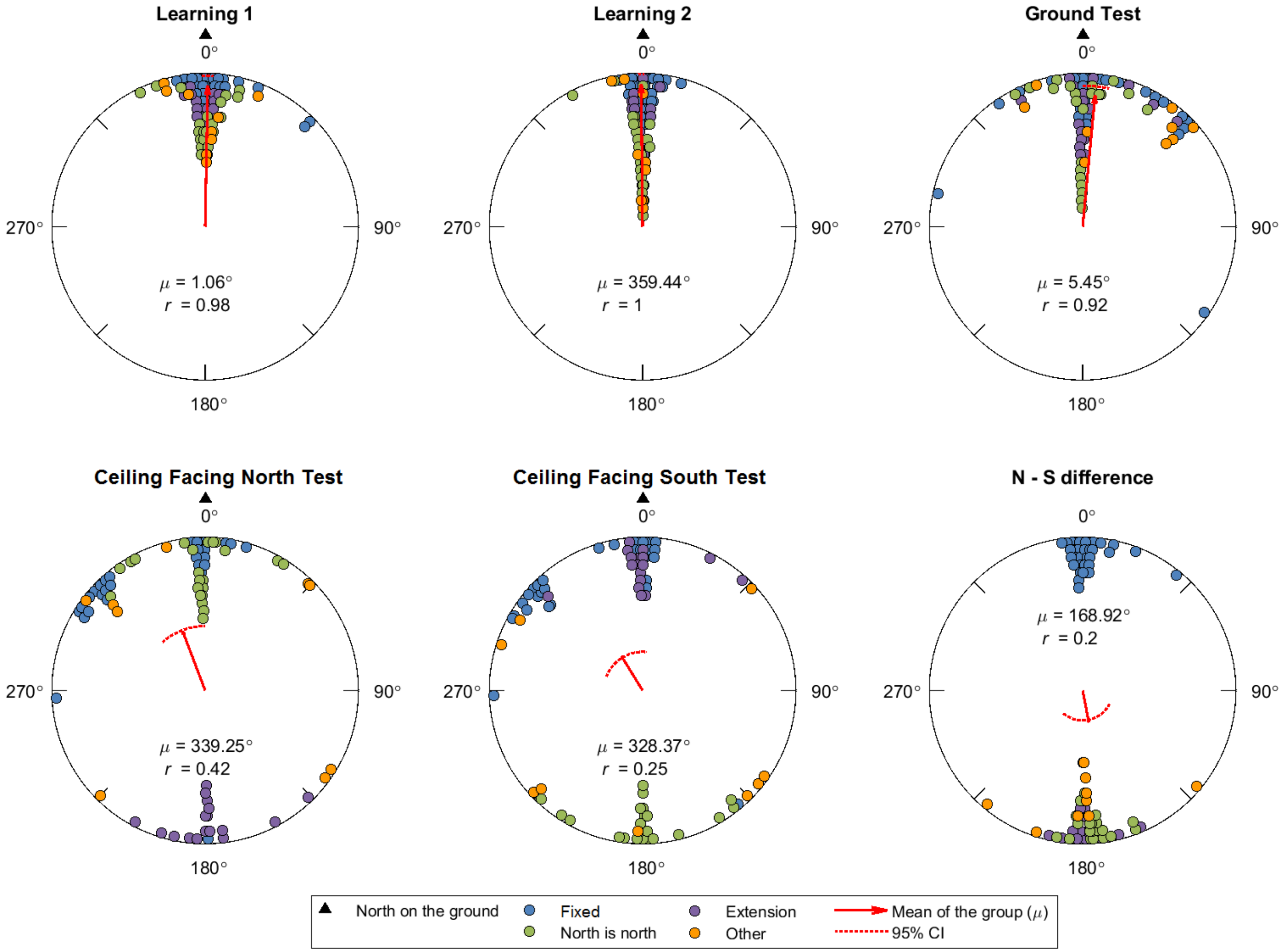
Learning 1
0°
90°
180°
270°
μ = 1.06°
r = 0.98
Learning 2
0°
90°
180°
270°
μ = 359.44°
r = 1
Ground Test
0°
90°
180°
270°
μ = 5.45°
r = 0.92
Ceiling Facing North Test
0°
90°
180°
270°
μ = 339.25°
r = 0.42
Ceiling Facing South Test
0°
90°
180°
270°
μ = 328.37°
r = 0.25
N - S difference
0°
90°
180°
270°
μ = 168.92°
r = 0.2
▲ North on the ground
● Fixed
● North is north
● Extension
● Other
Mean of the group (μ)
95% CI

Figure 3.10. Estimated heading (H') and angular difference in Experiment 4 (placement task on the ceiling). Each dot indicates the H' for one participant. The blue dots represent the participants in the "fixed" category. The green dots represent the participants in the "north is north" category. The purple dots represent the participants in the "extension" category. The orange dots represent the participants in the "other" category. The black triangle indicates North on the ground (0°). The red arrow indicates the circular direction (μ) and the length (r) of the mean vector of the H' across all participants. The arc above the mean direction indicates the 95% confidence interval of the mean direction.

For the JRD tests, we calculated the averaged absolute pointing error and the response latency for each participant and then calculated the mean for the whole group. The mean and standard deviation for the absolute pointing error and the response latency were shown in Table 3.5.

Response latency as a function of the physical facing direction (North, South) and imagined heading direction (North, South) is plotted in Figure 3.11. The absolute pointing error showed the same general pattern as the angular error. There was no evidence of speed-accuracy trade-offs. For brevity, here we only report the results from the statistical tests using response latency as the dependent variable.

Table 3.5. *Mean and standard deviation for absolute pointing error and response latency in the JRD task in Experiment 4.*

Ceiling facing direction	**Imagined direction**	**Absolute pointing error (°)**	**Response latency (seconds)**
		Mean (*SD*)	*Mean* (*SD*)
North	North	35 (19.51)	4.60 (3.20)
North	South	40 (24.78)	4.87 (3.50)
South	North	38 (23.00)	4.48 (2.77)
South	South	42 (25.49)	5.44 (3.68)

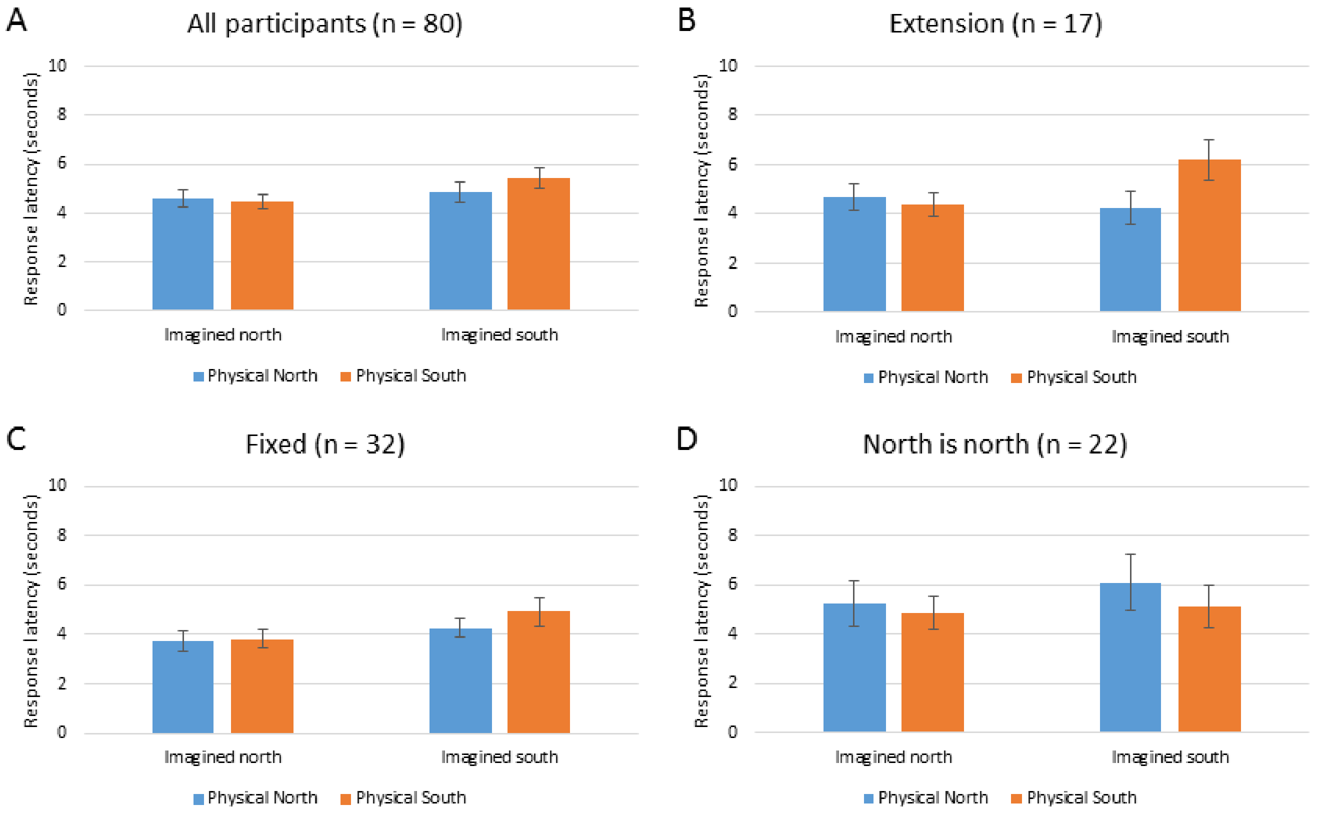
A
All participants (n = 80)
Response latency (seconds)
10
8
6
4
2
0
Imagined north
Imagined south
🟦 Physical North
🟧 Physical South
B
Extension (n = 17)
Response latency (seconds)
10
8
6
4
2
0
Imagined north
Imagined south
🟦 Physical North
🟧 Physical South
C
Fixed (n = 32)
Response latency (seconds)
10
8
6
4
2
0
Imagined north
Imagined south
🟦 Physical North
🟧 Physical South
D
North is north (n = 22)
Response latency (seconds)
10
8
6
4
2
0
Imagined north
Imagined south
🟦 Physical North
🟧 Physical South

Figure 3.11. Response latency in Experiment 4 (JRD task on the ceiling). Panel A shows the results for all the participants. Panels B, C and D show the results for each category of participants according to the placement task results. Error bars represent standard errors of the mean.

A 2 × 2 repeated-measure ANOVA (Physical Facing Direction [North, South] × Imagined Heading Direction [North, South]) was conducted. There was no significance in the main effects of physical facing direction and imagined heading direction, or the interaction (ps > .24, partial $\eta^2 < .05$).

As in Experiment 3, participants were categorized according to their responses in the ceiling tests (see Table 3.2 and Figure 3.10). There were 32 people in the “fixed” category (40%), 22 people in the “north is north” category (27.5%), and 17 people in the “extension” category (21.25%). Nine participants (11.25%) were categorized as “other.”

For each category, we conducted a 2 × 2 repeated-measure ANOVA (Physical Facing Direction [North, South] × Imagined Heading Direction [North, South]) with response latency as the dependent variable.

For the “fixed” participants, the main effect of imagined heading was significant, $F(1, 31) = 7.19$, $p = .012$, partial $\eta^2 = .19$. Imagining north was faster than imagining south regardless of the physical facing direction, which indicates a memory effect. But there were no sensorimotor effect [main effect of physical facing: $F(1, 31) = 1.59$, $p = .217$, partial $\eta^2 = .05$; interaction: $F(1, 31) = 0.97$, $p = .332$, partial $\eta^2 = .03$]. These results indicate that the “fixed” participants directly retrieved a fixed heading from memory they acquired from the ground phases.

For the "north is north" participants, there was no significant main effect or interaction (*p*s > .23, partial $\eta^2 < .07$). Therefore, there was no sensorimotor alignment effect for the "north is north" participants.

For the "extension" participants, the main effect of physical facing direction was marginally significant, $F(1, 16) = 3.32$, $p = .087$, partial $\eta^2 = .17$. There was also a significant interaction effect between physical facing direction and imagined heading, $F(1, 16) = 8.25$, $p = .011$, partial $\eta^2 = .34$. Further analysis showed that for the imagined south condition, the responses were significantly faster when these participants physically faced north on the ceiling than when they faced south, which indicates a reversed sensorimotor alignment effect, $t(16) = 4.53$, $p < .001$, Cohen's $d = 1.55$. Cohen's *d*s were calculated as $t \times \sqrt{\frac{2}{N}}$ where N denotes the number of participants. This indicates that participants extended their heading on the ground to the ceiling by a pitch of 180° so that their allocentric heading of facing the same direction on the ceiling and the ground were opposite, producing the reversed sensorimotor alignment effect.

The consistent findings from the placement and JRD tasks once again confirm the reliability of categorizing participants in terms of their heading based on the placement task.

3.7 Experiment 5

The purpose of Experiment 5 was to demonstrate that the sensorimotor alignment effect could be used to examine participants' heading on the ground. Although previous studies indicated that the sensorimotor alignment effect is a powerful tool to examine whether participants updated the allocentric heading (Kelly, Avraamides, & Loomis, 2007; Mou, McNamara, Valiquette, & Rump, 2004; Shelton & Marchette, 2010), Experiment 5 was conducted to make sure it is still a good tool in our experimental setup.

3.7.1 Method

3.7.1.1 Participants. 32 university students participated in the experiment (age range = 17–28 years, *M* = 19.22 years) with an equal number in each gender.

3.7.1.2 Apparatus and environment. They were the same as Experiment 2.

3.7.1.3 Design and materials. They were the same as Experiment 2 except that the wall JRD tests were replaced by the ground JRD tests. The JRD trials were exactly the same as those used in Experiment 2. During the ground JRD phase, the platform was presented at either the north or the south of the mat on the ground. Each participant received two JRD tests with north and south physical facing directions. The testing order of the ground JRD phases was counterbalanced across participants.

3.7.1.4 Procedure. The procedure for Experiment 5 was exactly the same as for Experiment 2 with the following exceptions. The participants did not practice navigating on the wall or on the ceiling. On each ground JRD test, the participants navigated to the platform and faced the mat, and then did the JRD task.

3.7.2 Results and discussion

We calculated the averaged absolute pointing error and the response latency for each participant and then calculated the mean for the whole group. Table 3.6 shows the mean and standard deviation for the absolute pointing error and response latency.

Response latency as a function of physical facing direction (North, South) and imagined heading direction (North, South) is plotted in Figure 3.12. The absolute pointing error showed the same general pattern as the angular error. There was no evidence of speed-accuracy trade-offs. For brevity, here we only report the results from the statistical tests using response latency as the dependent variable.

Table 3.6. *Mean and standard deviation for absolute pointing error and response latency in the JRD task in Experiment 5.*

Physical facing direction	**Imagined direction**	**Absolute pointing error (°)**	**Response latency (seconds)**
		Mean (*SD*)	*Mean* (*SD*)
North	North	38 (19.29)	3.04 (1.21)
North	South	45 (26.42)	5.22 (2.37)
South	North	50 (29.29)	4.72 (2.80)
South	South	35 (25.21)	3.52 (2.18)

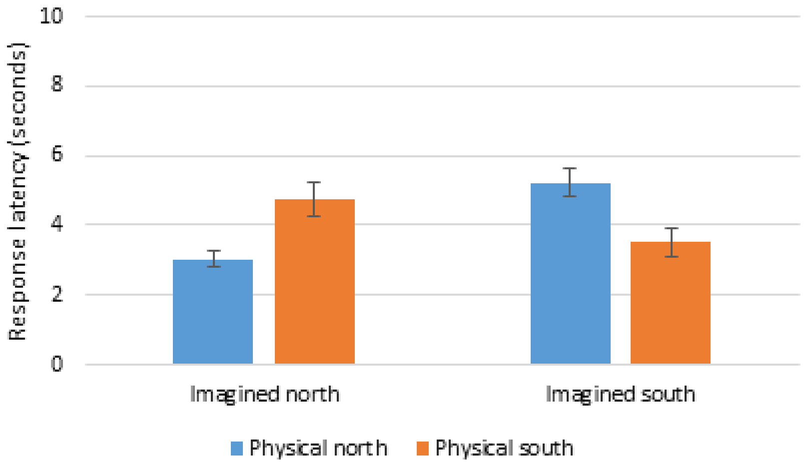

Figure 3.12. Response latency in Experiment 5 (JRD task on the ground). Error bars represent standard errors of the mean.

A 2 × 2 repeated-measure ANOVA (Physical Facing Direction [North, South] × Imagined Heading Direction [North, South]) was conducted. There was no significance found in the main effects of physical facing direction and imagined heading direction (*p*s > .07, partial η^2

< .10). There was a significant interaction effect between physical facing and imagined heading, $F(1, 31) = 20.03$, $p < .001$, partial $\eta^2 = .39$. Further analysis showed that for the imagined south condition, the responses were significantly faster when these participants physically faced south than when they faced north, $t(31) = 3.79$, $p = .001$, Cohen's $d = 0.95$, whereas for the imagined north condition, the responses were significantly faster when these participants physically faced north than when they faced south, $t(31) = 3.70$, $p = .001$, Cohen's $d = 0.93$. The performance was always better when the imagined direction was the same as the physical facing direction, which indicates a sensorimotor effect.

In Experiment 5, we replicated previous findings about the sensorimotor alignment effect in the JRD task on the ground (Kelly et al., 2007; Mou et al., 2004; Shelton & Marchette, 2010). The results suggest that the sensorimotor alignment effects could be used to examine participants' updated heading on the ground. In addition, participants could successfully update their allocentric heading on the same plane as the learning phase (i.e., the ground) as indicated by the ground test for replacing objects in the previous experiments.

3.8 General discussion

The current study investigated whether humans can spontaneously update allocentric headings in self-locomotion with pitch rotations. In particular, we tested three hypotheses, the extended-allocentric-heading hypothesis, the allocentric-facing-direction hypothesis, and the fixed-heading hypothesis (see Table 3.1). Participants conducted a placement task and a JRD task either on the wall or the ceiling after locomoting from the ground. Consistent across experiments and across tasks, we found that the participants could be grouped into three different categories (see Table 3.2), each corresponding to one of the three hypotheses.

Most importantly, only about 20% of the participants (the “extension” category, see Table 3.2) extended their allocentric heading from the ground to other planes. Their responses in both the placement and JRD tasks were consistent with the extended-allocentric-heading hypothesis. In the placement task, they treated the direction of Up on the north wall as the direction of North on the ground and the direction of Up on the south wall as the direction of South on the ground (Experiment 1); they treated the direction of north on the ceiling as South on the ground and the direction of south on the ceiling as North on the ground (Experiments 3 and 4). In the JRD tasks on the ceiling, they showed a reversed sensorimotor alignment effect, suggesting that they treated their heading of facing north on the ceiling as the heading of facing South on the ground (Experiment 4). Note that in all experiments, the participants did not receive any explicit instructions about how to update their allocentric headings on the walls and on the ceiling. As the percentage in this category was only about 20%, for the majority of human participants, extending the 3D allocentric heading from the ground to the walls and the ceiling may not be spontaneous.

As a striking comparison, most participants could spontaneously update their headings on the ground as shown in the ground placement tests (Experiments 1, 3, and 4) and the ground JRD task (Experiment 5). In particular, they could accurately recover the reference direction that had been used to encode objects’ locations (e.g., north) to reconstruct the objects layout accurately from a new perspective in the ground tests. For most participants, the estimated headings (H’) corresponding to facing north in the ground test were very close to the north direction on the ground (Figures 3.5, 3.6, 3.8-3.10). In the ground JRD task, participants performed better for an imagined heading (e.g., imagined north in Figure 3.12) when their physical facing direction (e.g., physical north) was same as the imagined heading rather than when their physical facing direction (e.g., physical south) was different from the imagined heading. This sensorimotor alignment effect clearly indicates that participants update their heading when they turn their body (i.e., yaw) on the ground (e.g., Kelly et al., 2007).

Therefore, the difficulty of updating the 3D heading in the current study occurred during the locomotion from the ground to the walls and the ceiling by pitch but not during turning body on the ground by yaw. One critical difference between the yaw and pitch rotations in the current study is the idiothetical information that was available in the former but not in the latter. When participants yawed on the ground, they physically turned their body so the idiothetical information provided rotational information in addition to the visual cues. In contrast, participants, while pitching between two planes, only perceived their rotation from the visual cues. Thus, one may argue that for humans, spatial updating during pitch between planes might not be harder than that during yaw on the ground. The current finding of more difficult spatial updating during pitch between planes occurred only because the visual information from pitch rotation was not sufficient for spatial updating. This concern is reasonable as idiothetical cues (e.g., proprioceptive and vestibular systems) are important to spatial orientation and updating (Klatzky et al., 1998; Rieser, 1989; Ruddle, Volkova, & Bülthoff, 2011). Future research should examine participants who physically pitch in the real environments with gravity as a cue to indicate the changes in body position. However, some previous studies have showed that in a familiar environment with rich landmark cues, visual information is sufficient for spatial orientation and updating of yaw rotations on the ground (Riecke, Cunningham, & Bülthoff, 2007). In our experiments, rich visual information about orientations was provided by the geometry of the room and the landmarks inside the room (e.g., the lights on the ceiling and the furniture at the corners).

Furthermore, significant numbers of participants in the current experiments did use visual information to correctly identify their facing direction although they did not extend their headings from the ground to other planes. A relatively large percentage of participants (about 25%, the “north is north” category in Experiments 3 and 4) always knew the directions of north and south on the ceiling but did not successfully encode the transformation relationship between the planes via pitch rotations. Their responses in the placement task indicate that these participants treated the north direction on the ceiling as the north direction on the ground and also treated the south direction on the ceiling as the south direction on the ground. This finding suggests that they did update their heading using the visual information. However, they might only have updated the 2D heading rather than the 3D heading. If they had established the 3D heading, they would have shown sensorimotor alignment effects in JRD tasks as did the extension group. In particular, they should have shown the typical sensorimotor alignment effect that performance for an imagined heading (e.g., imagined north) should be better when their physical facing direction (e.g., physical north) was the same as the imagined heading than when their physical facing direction (e.g., physical south) differed from the imagined heading.

Why could the participants in the “north is north” category not use the visual information to establish a 3D heading? According to the allocentric-facing-direction hypothesis, humans as a species locomote mostly upright on the ground. Thus, their facing direction is always consistent with their allocentric heading. For example, for an upright individual on the ground, facing north means their heading is north. Therefore, humans might just use their facing direction as their allocentric heading and not realize that their allocentric headings would change if they were upside down, even if in that position they still faced the same direction. Therefore, they might have kept using their facing direction as their heading even on the other planes. Hence, the responses of the “north is north” category suggest that updating the 3D heading on the ceiling was difficult not just because of the experimental designs in the current study, which made it impossible for participants to recognize allocentric directions using visual information in the environment. Instead, it was due to the intrinsic difficulty of updating the 3D heading after pitch rotations.

The “fixed” category of participants also found it difficult to update 3D headings after pitch rotations. About 43% of the participants in the rotation group (Experiments 3 and 4) showed a “fixed” type of responses in the placement task, and also a fixed preferred imagined heading in the JRD task regardless of their physical facing directions.

The “fixed” participants did not have 3D allocentric headings as they did not show any sensorimotor alignment effect in JRD tasks (Experiment 4). We speculate that they did not even establish their 2D heading using the allocentric directions, as their placement responses were the same while facing South and facing North. As most humans do not have experiences in pitching from the ground to the ceiling, this group of participants might not have been able to use the environmental cues to orient themselves on the ceiling and thus had to retrieve memories to do the tasks. The responses of these participants were consistent with the fixed-heading hypothesis.

The extended-allocentric-heading hypothesis was derived from the findings of bats and rats and the toroidal model (Finkelstein et al., 2015; Page et al., 2018; Taube et al., 2013). As only 20% of the participants extended their heading via locomotion involving pitch rotations in the current study, this finding suggests that updating the human 3D heading, unlike bats and rats, does not fit the toroidal model (Finkelstein et al., 2015; Taube et al., 2013). The difference between species may be explained from the evolutionary perspective. Bats and rats have extensive experience of physical pitch rotations as such movements are essential to their survival, whereas humans have very few such experiences. Humans spend most of their time "upright" during locomotion. The body structure of humans is different from that of bats and rats in that our facing direction is actually perpendicular to our body's long (head-foot) axis whereas the facing direction in rats is parallel to their bodies' long axis. Therefore, even in ancient times, when humans climbed on trees or mountains to hunt or gather, their bodies were still upright most of the time. By contrast, bats and rats frequently transform between different planes in a 3D environment using pitch rotations. Bats have to pitch 180° to hang upside down on the ceiling of a cave; therefore their heading representation may be extended in all 360° pitch rotations. Different neural and cognitive mechanisms are developed to accommodate the natural locomotion style for different species. Thus, for humans, locomotion onto walls or ceilings by pitching did not sufficiently update their 3D heading.

This evolutional explanation is consistent with several other findings. Previous research has shown that although rats do pitch rotations very often, they usually do not have to pitch more than 90° to forage; therefore their heading may not be accurate when locomoting inverted on the ceiling (Calton & Taube, 2005). The difference between bats and rats further supports the evolutional explanation. In addition, this evolutional explanation is consistent with our findings that most participants spontaneously updated their heading during yaw rotations on the ground and that participants in the "north is north" category treated their facing direction as their allocentric heading while being tested on the ceiling, as discussed above.

The current study also showed a huge individual difference in the 3D allocentric headings among the participants, as there were three different categories of participants. In the current study, we did not collect any variables related to individual differences except gender (but no gender difference was significant in either JRD tasks or placement tasks in any of the experiments). Therefore, we are not sure about the origins of the individual differences in updating 3D headings.

We speculate that individuals' physical experience of pitch rotations might contribute to the individual differences observed in the current study, as training can improve spatial abilities (Feng, Spence, & Pratt, 2007). For example, participants who practiced gymnastics might have more experiences in pitch rotations of their body. To examine the role of individuals' physical experience of pitch rotation in updating 3D headings, future research may test some athletes, jet pilots, and astronauts who do a lot of training with physical pitch and roll rotations. Such research might examine whether these people more likely extend their 3D heading from the ground to walls and the ceiling using the experimental paradigm of the current study. We may also test whether human infants more likely update their heading of yaw rotation before and after they start crawling, which might be a crucial time point for the development of spatial ability (Crowther, Lew, & Whitaker, 2000).

One further interesting question is whether humans can update allocentric headings via roll rotations in self-locomotion. Intuitively, updating heading via roll rotations might be even harder than via pitch for humans as humans usually do not have such experience in daily locomotion. One study suggests that monkeys may have head direction cells that are tuned to roll rotations (Laurens, Kim, Dickman, & Angelaki, 2016). It is likely that humans also have head direction cells that are sensitive to roll rotations. However, on a behavioral level, updating allocentric headings in roll rotations might involve more cognitive efforts than in pitch rotations. Clearly, more research is needed in this area to further understand the mechanisms in 3D heading representations and updating on both the neural and behavioral levels.

3.9 Conclusion

The findings of the current study showed that on a behavioral level, for the majority of human adults, the allocentric heading on vertical and inverted planes is not an extension of that on the ground. Among these people, some used their facing direction (e.g., north or gravity up) as their heading whereas others directly retrieved a fixed heading from their memories. The current study provides new empirical evidence about 3D allocentric heading updating in humans and suggests that evolutionary and individual histories of locomotion in natural environments may account for the differences in updating 3D headings between humans and non-human animals (i.e., rats and bats).

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3.11 Supplementary materials

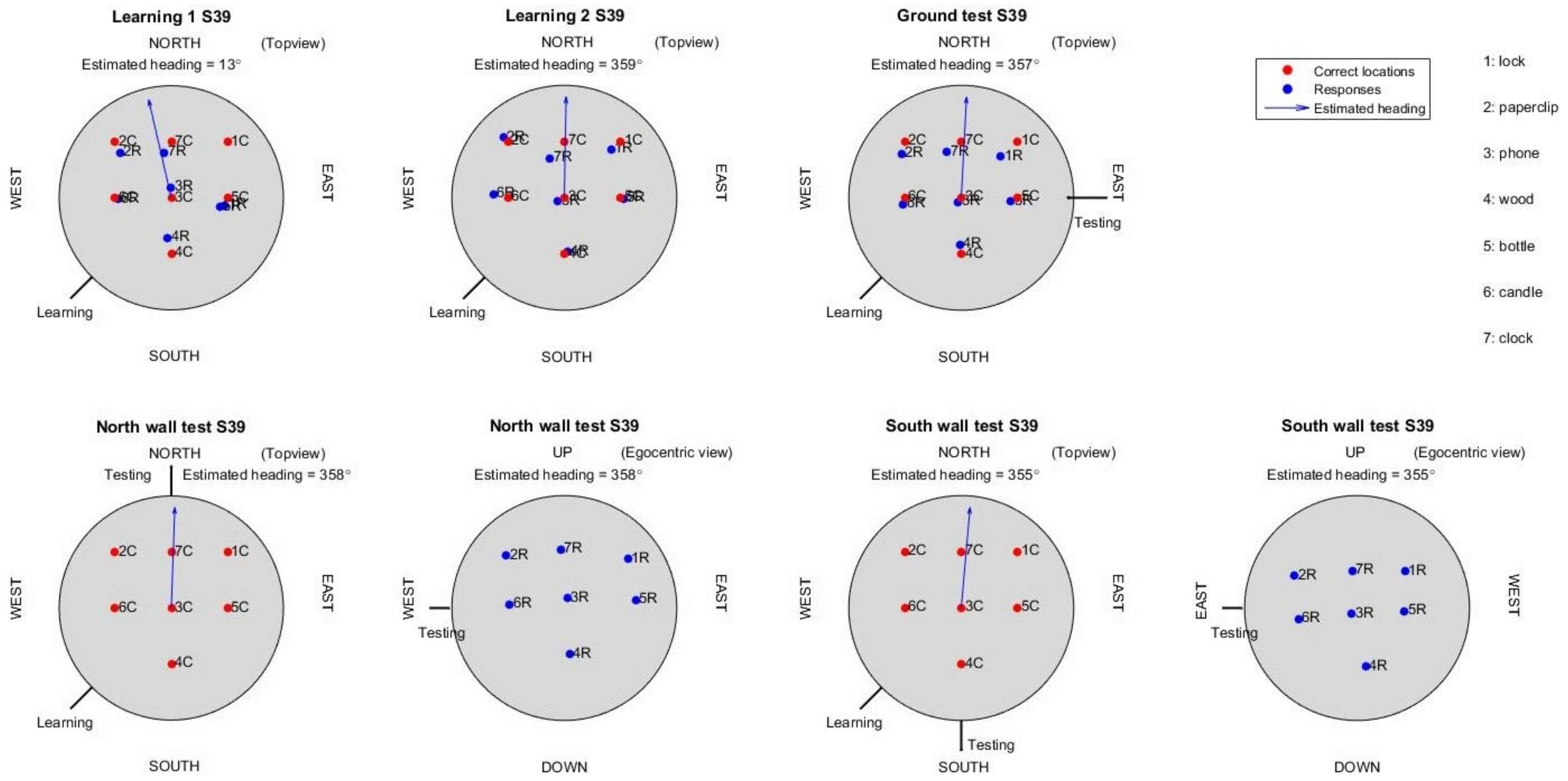
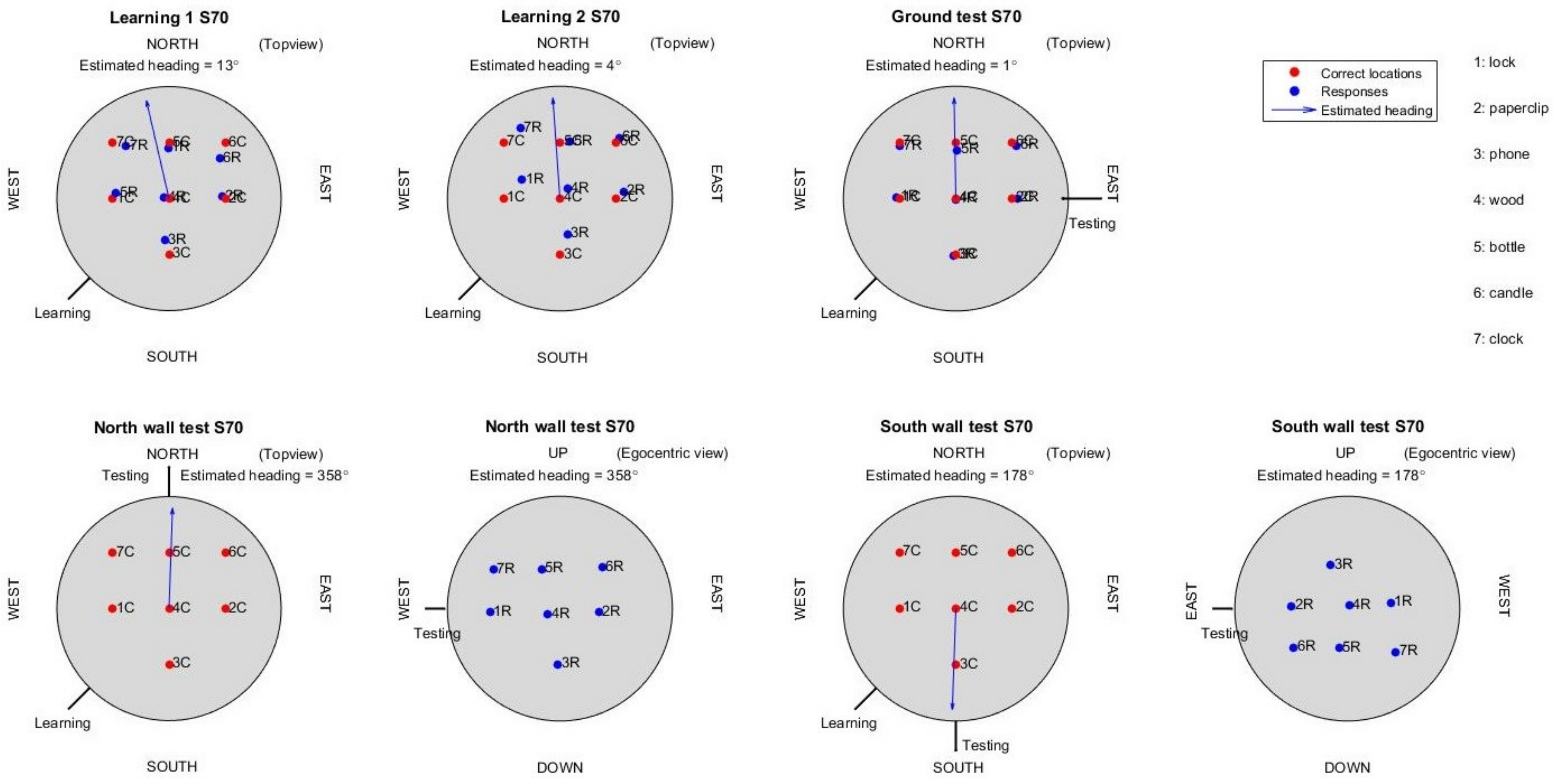


Figure S1. Representative responses of the “same-up” category from a participant in the rotation group in Experiment 1. Blue arrows denote the estimated directions that correspond to North on the ground in the learning phase and the ground test and to Up on the wall in the wall tests.



Learning 1 S70

Learning 2 S70

Ground test S70

North wall test S70

North wall test S70

South wall test S70

South wall test S70

Figure S2. Representative responses of the “extension” category from a participant in the rotation group in Experiment 1. Blue arrows denote the estimated directions that correspond to North on the ground in the learning phase and the ground test and to Up on the wall in the wall tests.

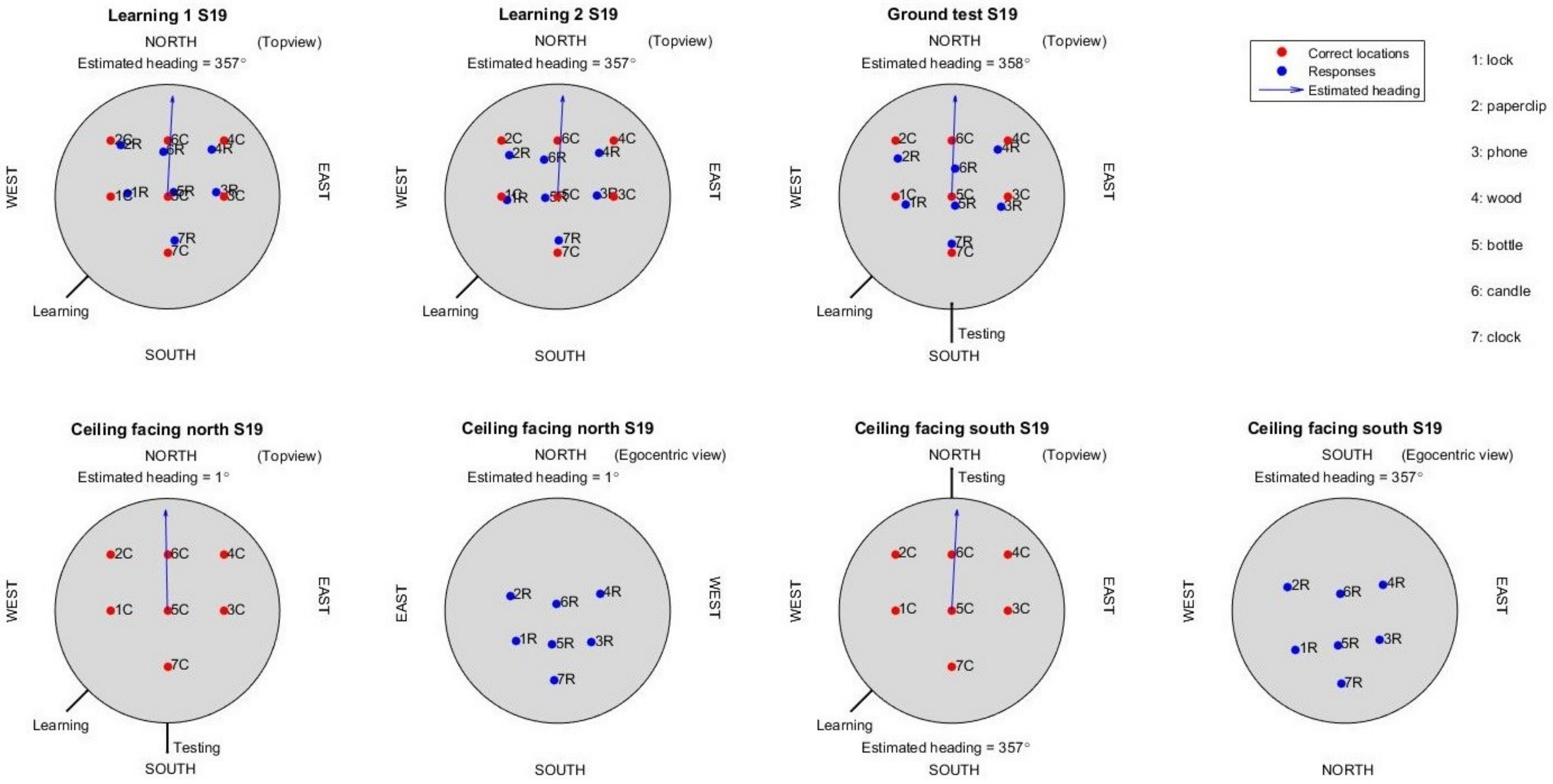


Figure S3. Representative responses of the "fixed" category from a participant in the rotation group in Experiment 3. Blue arrows denote the estimated directions that correspond to North on the ground in the learning phase and the ground test and to North on the ceiling in the ceiling tests.

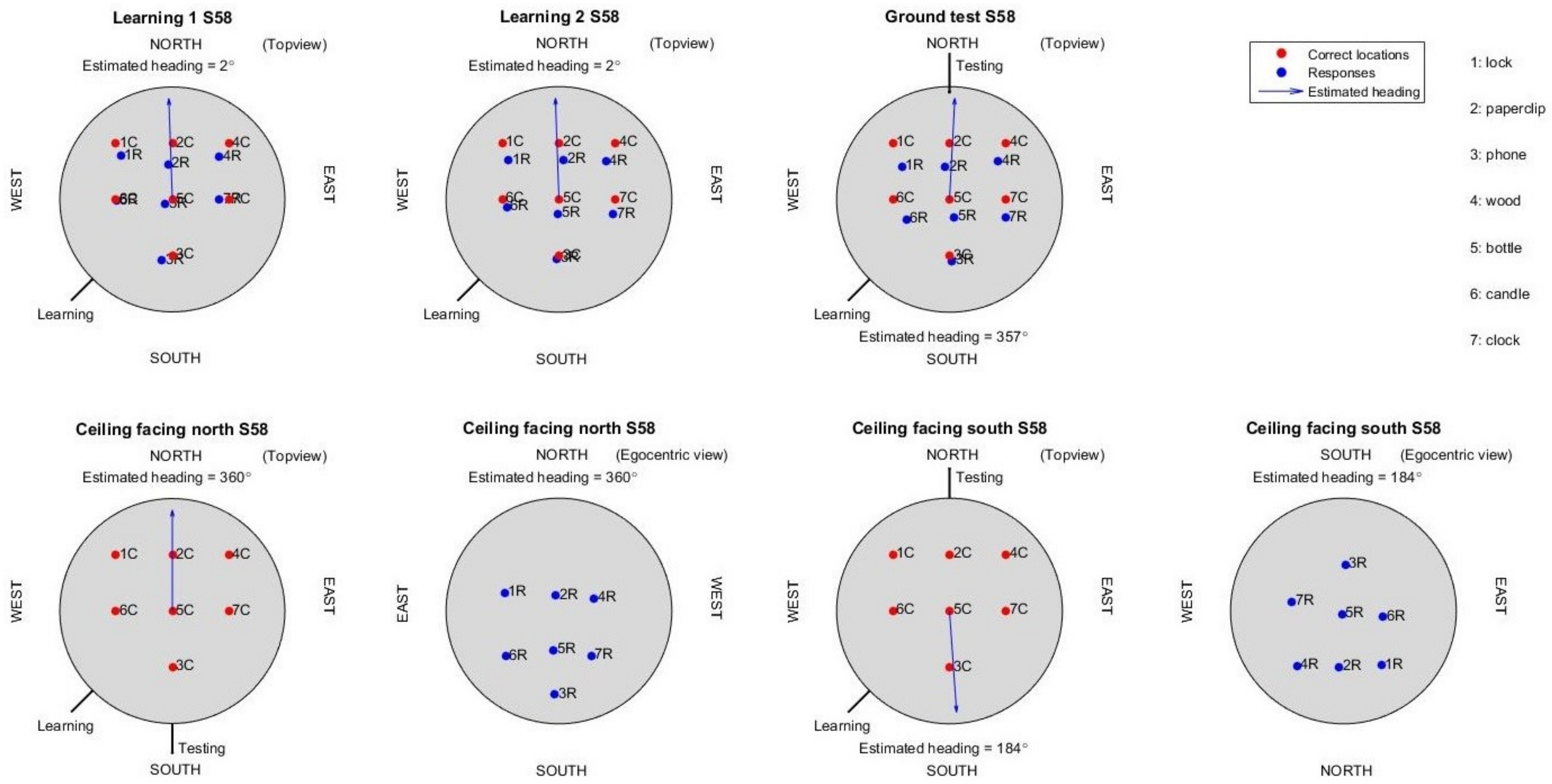
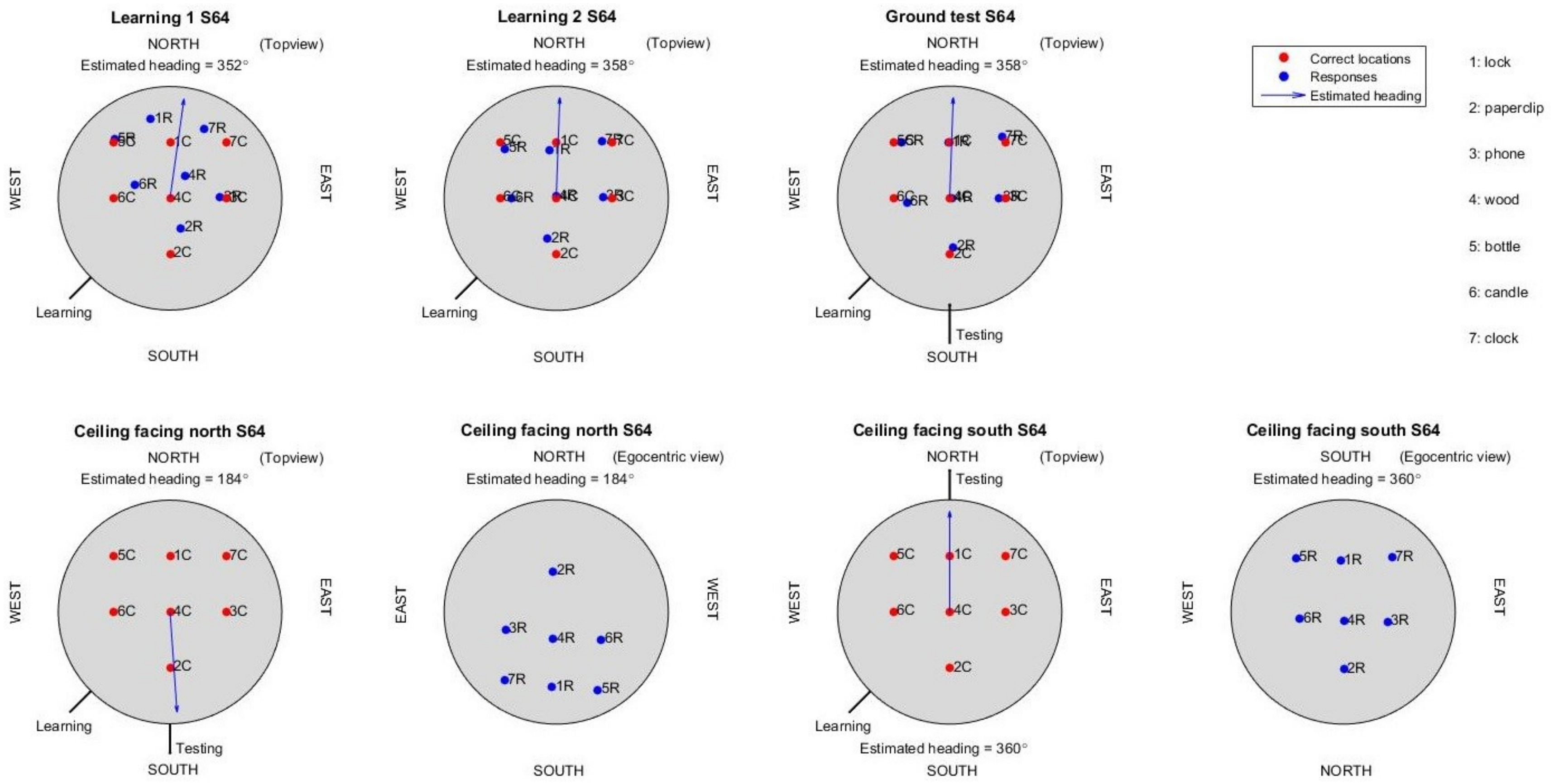


Figure S4. Representative responses of the "north is north" category from a participant in the rotation group in Experiment 3. Blue arrows denote the estimated directions that correspond to North on the ground in the learning phase and the ground test and to North on the ceiling in the ceiling tests.


Learning 1 S64

Learning 2 S64

Ground test S64

Ceiling facing north S64

Ceiling facing north S64

Ceiling facing south S64

Ceiling facing south S64

Figure S5. Representative responses of the "extension" category from a participant in the rotation group in Experiment 3. Blue arrows denote the estimated directions that correspond to North on the ground in the learning phase and the ground test and to North on the ceiling in the ceiling tests.

Chapter 4 General discussion

The world is three-dimensional. In many situations, it is navigable. Previous research has provided numerous evidence about spatial navigation on 2D surfaces whereas how animals represent space in 3D navigation involving vertical information is much less often investigated (Jeffery, Jovalekic, Verriotis, & Hayman, 2013; Jeffery, Wilson, Casali, & Hayman, 2015). The current dissertation work aims to provide new evidence to understand humans' spatial representation mechanisms in 3D navigation. Chapters 2 and 3 present two studies examining 3D location memory and 3D heading updating. In Chapter 4, I first summarize the findings in the two studies and then discuss the implications by these findings.

4.1 Review of the experiments

Study 1 in Chapter 2 investigated whether humans' localization is more variable vertically than horizontally in different locomotion modes. Participants localized targets on a vertical wall via self-locomotion. One group of participants flew three-dimensionally along their viewing direction towards the target (flying group). The second group only locomoted on the floor and the wall along the projection of the viewing direction onto the current travelling surface (climbing group). The third group pressed a button to be teleported from the floor to the wall and then locomoted along the wall (teleportation group). Both the flying and the climbing groups showed a horizontal advantage of location memory whereas the teleportation group showed a vertical advantage. The trajectories of the participants indicate a vertical advantage of locomotion on a vertical surface. The results suggest that locomotion mode does not account for the horizontal advantage for the surface-travelling animals. Therefore, the horizontal advantage is more likely to be species-specific rather than locomotion-mode specific.

Study 2 in Chapter 3 investigated humans' 3D heading updating in a placement task and a JRD task. Experiments 1 and 2 examined the updating of allocentric heading via a 90° pitch rotation from the ground to the vertical walls. Experiments 3 and 4 examined the updating via 180° pitch rotations from the ground to the ceiling. Consistently found across tasks and experiments, only about 20% of the participants spontaneously updated their allocentric heading from the ground to the vertical planes (walls) or to the inverted plane (ceiling) via pitch rotations (the "extension" category). The majority of the participants either used their facing direction as their heading (the "north is north" category) or directly retrieved a fixed heading from their memories (the "fixed" category). Experiment 5 showed that the sensorimotor alignment effect in the JRD task can be used as an effective tool to examine 3D allocentric heading updating. These results indicate that on a behavioral level, only a small portion of humans can spontaneously represent 3D allocentric headings via pitch rotations while most humans only represent 3D allocentric directions (e.g., North, Up). Therefore, the toroidal (extension) model proposed previously according to the findings in bats and rats (Finkelstein et al., 2015; Page et al., 2018; Taube et al., 2013) may not be applicable to humans.

4.2 Implications by the current studies

The two studies in this dissertation shed light on the mechanisms of humans' spatial representation, especially those formed in 3D navigation. In the following sections, I discuss three aspects that are implied by the current findings.

4.2.1 Is the cognitive map three-dimensional?

Since Edward Tolman proposed the concept "cognitive map" (Tolman, 1948), numerous research has been conducted to explore the spatial learning and memory of animals across species and experimental methodologies. One of the significant findings from recording of neuron firing patterns in animals' brain is that the place cells in the hippocampus are responsible for processing the location information, which is essentially the "cognitive map" in the brain

(O’Keefe & Dostrovsky, 1971; O’keefe & Nadel, 1978). Following research has demonstrated that the place cells not only respond to horizontal displacements, but also to vertical displacements (Hayman, Verriotis, Jovalekic, Fenton, & Jeffery, 2011; Jeffery, Anand, & Anderson, 2006; Knierim & McNaughton, 2001; Knierim, McNaughton, & Poe, 2000; Yartsev & Ulanovsky, 2013). These findings suggest that the cognitive map may not be purely 2D as intuitively speculated or as the term “map” suggested to be similar to the 2D maps used in real life. However, the place cells seem to fire in different variabilities in horizontal and vertical dimensions (Hayman et al., 2011), which suggests that the cognitive map in the brain may not be equally accurate or precise in both horizontal and vertical dimensions. Previous researchers also have proposed that spatial representations in three-dimensional world seem to be a set of 2D, planar encoding rather than a 3D, volumetric one (Jeffery et al., 2013, 2015).

Study 1 in the current dissertation work further supports this idea that the participants showed the horizontal advantage in location memory as shown in previous studies and the advantage was not modulated by locomotion mode (the flying and the climbing groups). However, Study 1 also discovered that when the participants were not allowed to locomote across the horizontal floor, the horizontal advantage did not occur and the vertical variability was even smaller than the horizontal one (the teleportation group). These results highlight the importance of horizontal movements on the horizontal plane and also indicate that the cognitive map may not be elongated horizontally or vertically in all situations.

Therefore, human spatial representation is three-dimensional with unequal variance in horizontal and vertical dimensions. Extending the idea proposed by Jeffery and colleagues (Jeffery et al., 2013, 2015), there are two hypothetical structures of place fields in volumetric space (Figure 4.1). The place field is the discrete region of space where each place cell would fire (O'Keefe & Dostrovsky, 1971). The first possibility is that the place fields might have larger scale in vertical dimension than in horizontal dimension. The second possibility is that the place fields might have larger scale in horizontal dimension than in vertical dimension. The results in the current studies suggest that both possibilities are plausible although the former one may occur more frequently. The encoding accuracy may depend on the navigation requirements in specific tasks like navigating horizontally on the ground or on the vertical wall. Also the current study showed that the teleportation group had larger variance in both horizontal and vertical dimensions than the flying and the climbing groups. Therefore, in the second hypothetical structure, both horizontal and vertical dimensions may be more variable than those in the first possibility.

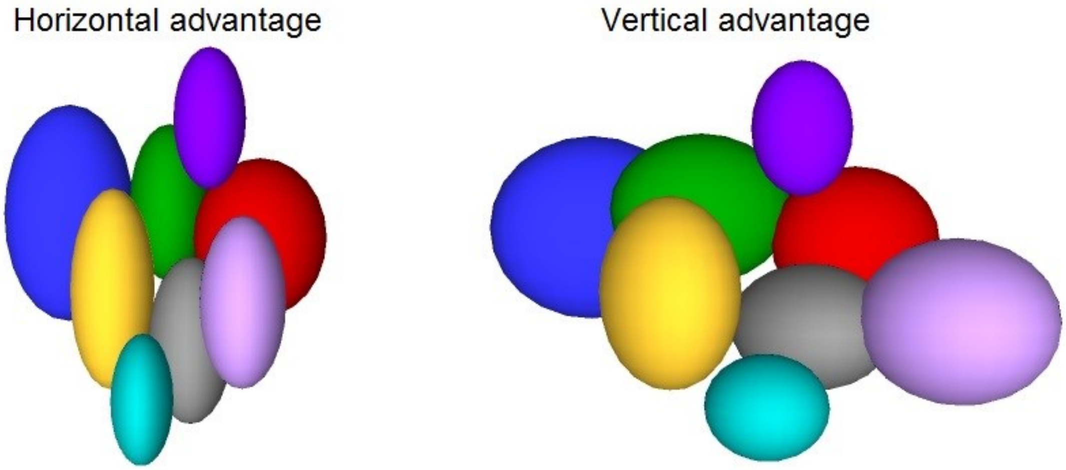


Figure 4.1. Hypothetical structure of place fields in volumetric space. Place fields might be volumetric, but have different scales in horizontal and vertical dimensions. The left panel shows a horizontal advantage. The right panel shows a vertical advantage.

One interesting question would be whether humans as 3D creatures can have any intuitive understanding of four-dimensional space which is beyond 3D environment properties and humans' usual navigation ability. Such a 4D space can be created by virtual reality technique and may not be visually pictured directly as it would be more like abstract, visual imagination. It has been shown that humans are able to make judgments about 4D virtual space (Ambinder, Wang, Crowell, Francis, & Brinkmann, 2009; Wang, 2014). Therefore, humans' spatial representations are not constrained to be three-dimensional by the evolution or development in the 3D world. It might be possible that humans may have evolved to have a more flexible cognitive mechanism in our brain than other animals for encoding locations although such flexibility may be evolved by sacrificing some locomotion ability (e.g., more difficult to locomote horizontally on the vertical wall than on the ground).

Linking this idea to the "species-specific" hypothesis in Study 1, it is possible that all mobile organisms might have evolved such a mechanism to get adapted to their living environments and survival manners. However, due to technical and practical issues, we probably cannot directly test this idea in non-human animals.

4.2.2 Spatial updating in yaw, pitch and roll

When an animal locomotes in the environment, it may change both its position and orientation. The animal's orientation relative to the allocentric reference system is termed as the allocentric heading (Klatzky, 1998). Being aware of the allocentric heading means that the animal knows the relationship between itself and the surrounding environment. Effective navigation depends on successful updating one's heading when one changes the orientation. Spatial updating on the horizontal ground is usually seen as an automatic process (Riecke, von der Heyde, & Bülthoff, 2005). On the horizontal ground, the allocentric heading is the same as the animal's facing direction. When the animal performs yaw rotations on the ground, it could update its allocentric heading using self-motion cues like vestibular system and external cues like landmarks. However, when the animal locomotes to other planes, especially via other forms of rotation (pitch and roll), the 3D allocentric headings cannot be specified by its facing directions but rather relate to its locomotion way. As discussed in Chapter 3, mental transformations are required in the updating process. For example, when the animal pitches 180° from being upright on the ground to being upside down on the ceiling, it has to mentally pitch backwards 180° to map its facing direction with its original heading on the ground (i.e., to update its heading). Otherwise, the animal would either ignore the pitch process and retrieve the memory on the ground or take the current facing direction indicated by environmental cues as its heading.

In Chapter 3, the differences between 3D allocentric directions and 3D allocentric headings have been presented and discussed. Essentially, heading means your moving direction in next step or action. Animals update their headings in 3D navigation in order to be prepared for their next action. For example, bats can fly into a cave upright and then perform a 180° pitch rotation to hang upside down on the ceiling of the cave. When the bats fly out of the cave, they perform a 180° pitch rotation to get back to the upright body position. They can update their heading via the pitch rotations. This mechanism has been possibly evolved because such information is essential for their survival. Bats need the information about where the entrance of the cave is in order to be prepared for flying out of the cave later.

In neural research, head direction cells are seen as the indication to show how an animal updates its heading in self-locomotion. It has been found that the head direction cells of rats and bats are tolerant to pitch rotations, which suggests that rats and bats may have extended, 3D allocentric headings (Finkelstein et al., 2015; Taube et al., 2013). A toroidal model has been proposed to explain these results (Finkelstein, Las, & Ulanovsky, 2016). According to this model, the firing pattern of the head direction cells would be similar to a section on a donut. The head direction system would be tuned to allocentric directions on the horizontal plane (e.g., when the animal yaws 180° from facing north to south) but not to changes caused by pitch rotations (e.g., when the animal pitches 180° from being upright on the ground to being upside down on the ceiling).

Study 2 showed that majority of humans cannot spontaneously update their allocentric headings in all three dimensions. These participants (i.e., the “fixed” and the “north is north” categories) could not spontaneously update their headings by mental pitch rotations whereas they had no difficulty to update heading by yaw rotations on the horizontal ground. This result suggests that humans may have different mechanisms for updating headings by yaw, pitch and roll, which are three essential transformations for forming 3D heading. The current findings seem inconsistent with the toroidal model (Finkelstein et al., 2016). For humans, the head direction system may not be able to encode all possible transformations between the navigable planes. In the current study, the participants were given opportunities to practice navigating on the vertical walls and on the ceiling. However, this practice lasted for only a few minutes. Anecdotally, many participants reported that they were new to movements in the virtual reality environment, especially to the pitch rotations. Thus, rare experience of 3D navigation may have led to the current results. Therefore, it seems that humans’ head direction system is not flexible enough to easily adapt to different situations or task demands.

As discussed in Chapter 3, the current study only presented visual stimuli during the pitch rotations whereas presented both visual and idiothedic cues during yaw rotations. Although previous research has demonstrated that visual information is sufficient to update one’s heading (Riecke, Cunningham, & Bülthoff, 2007), such results are based on 2D navigation with only yaw rotations. In 3D navigation, multi-sensory inputs might be fundamental for updating by pitch or roll. For example, when humans were blindfolded to roll, the gravity-dependent otolith and somatosensory cues facilitated them to get balanced after the roll (Vimal, DiZio, & Lackner, 2017; Vimal, Lackner, & DiZio, 2016). For pitch rotations, likewise, the gravity-dependent cues may carry a heavier weighting than the visual cues because visually performing pitch up or down without rotating the body head-foot axis happens a lot in daily life (e.g., looking straight up). It can be speculated that when the body head-foot axis rotates (roll or pitch), the gravity-dependent cues may play an important role in heading updating.

Future research is needed to examine this speculation. Here I propose a thought experiment. For example, participants could be tested in the virtual environment like in Study 2 but with idiothetic cues for pitch rotations. The participants could be physically upright when navigating on the horizontal ground. When the participants meet the boundary between the vertical wall and the horizontal ground, they could physically lie down on their back. That is, performing a physical 90° pitch rotation with both visual and idiothetic cues. Then the participants performed the JRD and the placement tasks. If this experiment showed that most people still could not extend their heading via pitch rotations, then the gravity-dependent cues may not be as important as speculated. If this experiment showed that a larger percentage of people could extend their heading than in Study 2, then the gravity-dependent cues may be crucial for 3D heading updating process.

4.2.3 Individual differences

The findings in the current studies also demonstrate the influences from evolutionary and personal histories on individual differences in 3D spatial representation.

Study 1 indicates that the horizontal advantage of location memory in encoding is not due to specific locomotion style (flying or surface-based locomotion) but more likely due to specific species. The current findings suggest that the horizontal movements on the horizontal ground lead to such advantage. As discussed above, humans might sacrifice some locomotion ability to evolve a better brain with a more flexible cognitive mechanism to function effectively in different situations. Evolutionarily, walking upright may provide humans the opportunity to have the better locomotion ability on the horizontal ground but, as a trade-off, the worse ability in the vertical dimension. When humans started to walk upright, navigating on vertical or steep surfaces like climbing a cliff would occur less often. Foraging or looking for shelters on the ground was undoubtedly sufficient. Similarly, the pitch and roll rotations as described in Study 2 may also be unusual if foraging was only on the ground. After humans went through the "cognitive revolution" and started to live around the world, hunting and gathering were the main jobs. When humans entered the agricultural society period, people were more likely to be bound to the piece of land they lived on. There would be more horizontal navigation on the ground and further less activities with vertical navigation, pitch and roll rotations, especially for people who lived in geographically flat regions. These changes may cause the evolution of the cognitive mechanism of spatial representations. In this sense, locomotion style shaped cognitive mechanisms. In turn, if the evolved, shaped cognitive mechanisms were in genetics of the offspring, then mental pitch and roll rotations would be more difficult for the offspring and thus the corresponding physical rotations would not be preferred. In this sense, the cognitive mechanisms shaped locomotion style. Certainly, these are only speculations based on the current findings. Anthropology research may provide more evidence for or against such speculations.

Study 1 also suggests that the vertical Euclidean distance can be used by humans in 3D navigation. Knowledge of geometry is believed to be one domain of the core knowledge across species (Spelke, Lee, & Izard, 2010). Although there are still ongoing debates about this theory, it is widely accepted that the ability to use geometry to orient emerges at very young age (for review, see Cheng, Huttenlocher, & Newcombe, 2013; Cheng & Newcombe, 2005). Specifically, the core knowledge theory proposes that the Euclidean distance information and the left/right sense are predominant properties to be used for navigation whereas the angular information is less dominant. For example, the ability to use angle information was shown at a later age in human children than distance and left/right sense (Hupbach & Nadel, 2005). However, the core knowledge theory seems to be silent on 3D spatial representation involving vertical dimension. Study 1 suggests that the distance information in vertical dimension can be encoded by human adults but with larger variability. In terms of angular information in vertical dimension, Study 2 suggests that the spontaneous use of vertical angles between horizontal plane and other planes may not be easy for humans. It is still unclear if the Euclidean properties in vertical dimension are included in the core knowledge but the current studies imply that these information may not be included. Developmental research is needed to answer this question.

Study 2 indicates that there are three types of responses which reflect three types of heading representation in humans. As discussed in Chapter 3, the origins of such individual differences are unknown (but it was not modulated by gender as no gender difference was found in the current studies). By contrast, Study 1 did not show any significant individual differences. Note that Study 1 provided all participants sufficient training/practice and only the data in the last three blocks were analyzed. Since training can improve spatial abilities (Feng, Spence, & Pratt, 2007), the practice phase may account for this difference across the two studies and no gender difference found in both studies.

To examine the origins of the individual differences, in addition to collecting information about the individual training experience of the participants, future research can use some classic spatial tests to examine the correlations between these tests and the tasks used in Study 2. First, perspective taking ability should be taken into account. In 2D (horizontal) navigation, perspective taking ability is found to be predictive to spatial abilities (Wolbers & Hegarty, 2010). Those tasks used in Study 2 require participants perform mental pitch rotations. This is similar to the idea in perspective taking tasks because the participants had to imagine themselves rotated (pitched) in the environment. Although classic perspective taking tests only require participants perform mental yaw rotations, there might be a strong correlation between the abilities of mental pitch and yaw rotations. Future research could use the perspective taking test to examine the correlation between this test and the task performance in Study 2. The results would tell us the relationship between abilities of mental pitch and yaw rotations.

Note that these rotations refer to *self* rotations, not object rotations. The classic 3D mental rotation test (Shepard & Metzler, 1971) is an example of object rotations, which includes all three possible ways of rotations. Clearly, mentally rotating objects in different ways is strongly correlated. Mentally manipulating objects seems to be more similar to object perception or navigation in small-scale environment. According to the core knowledge theory, there are two separate sub-systems that are responsible for navigation in large-scale and small-scale environments, respectively (Spelke et al., 2010). Future research could also use the 3D mental rotation test to examine the correlation between this test and the task performance in Study 2. The results would be important to find the origins of individual differences and to provide new evidence for or against the core knowledge theory in spatial domain.

4.3 Limitations and future directions

The current studies have a few limitations. First, both studies were conducted in virtual reality environments therefore the participants had no gravity-dependent cues. Especially in

Study 2, physical pitch rotations involving body-motion cues would provide the participants more information for the locomotion and may lead to more people demonstrating the extended representation. The apparatuses like those in previous gravity-roll studies (Vimal et al., 2017, 2016) might be used in future research to answer this question.

Second, both studies used behavioral tasks therefore the brain activation by vertical navigation and pitch rotation is not examined in the current studies. Although animal neural research has provided much evidence, humans may not have the same mechanisms due to species uniqueness. For example, as Study 2 suggests, humans do not fit the toroidal model (Finkelstein et al., 2016). Future research should use neuroscience methodology such as TMS and fMRI to investigate these questions.

Third, individual history information was not collected in the current studies. However, our results suggest that such information may be critical to explain the individual differences in Study 2. Therefore, future research should explore the topic with these information collected. One direction to go would be to test some athletes, flight jet pilots, scuba divers, and astronauts who do a lot of training with physical pitch and roll rotations and see whether they are more likely to extend their 3D heading from the ground to walls and the ceiling. A second direction to go would be from developmental perspective. Testing infants before and after they start crawling or toddlers before and after they start walking may reveal more on long-term individual history and its relationship with 3D spatial representation.

Fourth, so far only a few species have been examined about their 3D spatial representation and most studies were from the neurobiological perspective. Testing more other species with both neural and behavioral methods may provide more evidence on evolutionary experience in animals' navigation strategy.

Clearly, more research is needed to get a full picture across species about spatial representations in the three-dimensional world.

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