Spatial Memory and Spatial Orientation

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Abstract. Navigating through a remembered space depends critically on the ability to stay oriented with respect to the remembered environment and to reorient after becoming lost. This chapter describes the roles of long-term spatial memory, sensorimotor spatial memory, and path integration in determining spatial orientation. Experiments presented here highlight the reference direction structure of long-term spatial memory and suggest that self-position and orientation during locomotion are updated with respect to those reference directions. These results indicate that a complete account of spatial orientation requires a more thorough understanding of the interaction between long-term spatial memory, sensorimotor spatial memory, and path integration.

Keywords: Navigation; Path integration; Reorientation; Spatial cognition; Spatial memory; Spatial updating.

1 Introduction

Navigation through a familiar environment can be considered a two-part task, where the successful navigator must first orient him or herself with respect to the known environment and then determine the correct travel direction in order to arrive at the goal location. Several accounts of spatial memory and spatial orientation have been reported in recent years to explain human navigation abilities (Avraamides & Kelly, 2008; Kelly, Avraamides & Loomis, 2007; Mou, McNamara, Valiquette & Rump, 2004; Rump & McNamara, 2007; Sholl, 2001; Waller & Hodgson, 2006; Wang & Spelke, 2000). Inspired in part by perceptual theories positing separate representations for perception and action (Bridgeman, Lewis, Heit & Nagle, 1979; Milner & Goodale, 1995; Schneider, 1969), many of these theories of spatial memory agree that a complete account of human navigation and spatial orientation requires multiple spatial representations. The first such spatial representation is a long-term representation, in which locations are represented in an enduring manner. This long-term representation allows the navigator to plan future travels, recognize previously experienced environments, and identify remembered locations, even when those locations are obscured from view. The preponderance of evidence from spatial memory experiments indicates that these long-term representations are orientation dependent, with privileged access to particular orientations (see McNamara, 2003 for a review). Section 2 (below) reviews the evidence for orientation dependence, and also details recent experiments aimed at understanding the relevant cues that determine which orientations

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receive privileged access, particularly in naturalistic environments that contain many potential cues.

The second spatial representation consistently implicated in models of spatial memory is a working memory representation, referred to here as a sensorimotor representation, in which locations are represented only transiently. The sensorimotor representation is thought to be used when performing body-defined actions, such as negotiating obstacles and moving toward intermediate goal locations like landmarks, which can function as beacons. Because these behaviors typically rely on egocentrically organized actions, it makes sense that this sensorimotor representation should also be egocentrically organized, in order to maintain an isomorphic mapping between representation and response. The evidence reviewed in Section 3 supports this conjecture, indicating that the sensorimotor representation is organized in an egocentric framework. Although most models of spatial memory agree that the sensorimotor representation is transient, the exact nature of its transience is not well understood. While some experiments indicate that the sensorimotor representation fades with time (e.g., Mou et al., 2004), other evidence shows that the sensorimotor representation depends primarily on environmental cues that are only transiently available during locomotion (Kelly et al., 2007). Evidence supporting these two claims is presented in Section 3.

In order to stay oriented with respect to a known environment, the navigator must be able to identify salient features of his or her surrounding environment and match those features with the same features in long-term spatial memory. This point becomes particularly evident when attempting to reorient after becoming lost. For example, a disoriented student might have an accurate long-term representation of the campus, along with a vivid sensorimotor representation of his or her surrounding environment. But unless the student can identify common features shared by both representations, and bring those representations into alignment based on their common features, he or she will remain disoriented. Neither the sensorimotor nor the long-term representation alone contains sufficient information to re-establish location and orientation within the remembered space. Instead, the disoriented navigator must be able to align the long-term representation, which contains information about how to continue toward one's navigational goal, with the sensorimotor representation of the immediately surrounding space, similar to how visitors to unfamiliar environments will often align a physical map with the visible surrounds during navigation. In Section 4, we review previous work on cues to reorientation, and frame these results in the context of this matching process between long-term and sensorimotor representations. We also present new data from two experiments exploring the differences and similarities in spatial cue use during reorientation and maintenance of orientation, two tasks integral to successful navigation. The results suggest that spatial orientation is established with respect to the same reference directions that are used to organize long-term spatial memories.

2 Long-Term Spatial Memory

An every-day task like remembering the location of one's car in a stadium parking lot draws on the long-term spatial memory of the remembered environment. Because locations are inherently relative, objects contained in this long-term spatial memory must be specified in the context of a spatial reference system. For example, a football fan might remember the location of his or her car in the stadium parking lot with respect to the rows and columns of cars, or possibly with respect to the car's location relative to the main stadium entrance. In either case, the car's location must be represented relative to some reference frame, which is likely to be centered on the environment.

Much of the experimental work on the organization of long-term spatial memories has focused on the cues that influence the selection of one spatial reference system over the infinite number of candidate reference systems. In these experiments, participants learn the locations of objects on a table, within a room, or throughout a city, and are later asked to retrieve inter-object spatial relationships from the remembered layout. A variety of spatial memory retrieval tasks have been employed, including map drawing, picture recognition, and perspective taking. These retrieval tasks are commonly performed after participants have been removed from the learning environment, to ensure that spatial memories are being retrieved from the long-term representation and not from the sensorimotor representation. Here we focus primarily on results from perspective taking tasks, where participants point to locations from imagined perspectives within the remembered environment. A consistent finding from these experiments is that long-term spatial memories are typically represented with respect to a small number of reference directions, centered on the environment and selected during learning (see McNamara, 2003, for a review). During spatial memory retrieval, inter-object spatial relationships aligned with those reference directions are readily accessible because they are directly represented in the spatial memory. In contrast, misaligned spatial relationships must be inferred from other represented relationships, and this inference process is cognitively effortful (e.g, Klatzky, 1998). The pattern of response latencies and pointing errors across a sample of imagined perspectives is interpreted as an indicator of the reference directions used to organize the spatial memory, and a large body of work has focused on understanding the cues that influence the selection of one reference direction over another during acquisition of the memory.

Because we use our bodies to sense environmental information and also to act on the environment, the body's position during learning seems likely to have a large influence on selecting a reference direction. Consistent with this thinking, early evidence indicated that perspectives aligned with experienced views are facilitated relative to non-experienced views. This facilitation fell off as a function of angular distance from the experienced views (Diwakdar & McNamara, 1997; Roskos-Ewoldsen, McNamara, Shelton & Carr, 1999; Shelton & McNamara, 1997), and this pattern of facilitation holds true for up to three learned perspectives. These findings resonate with similar findings from object recognition (Bülthoff & Edelman, 1992), but are complicated by two other sets of findings. First, Kelly et al. (2007; see also Avraamides & Kelly, 2005) had participants learn a layout of eight objects within an octagonal room using immersive virtual reality. Participants freely turned and explored the virtual environment during learning, but the initially experienced perspective was held constant. After learning this layout, imagined perspectives aligned with the initially experienced perspective were facilitated, and this pattern persisted even after extensive experience with other perspectives misaligned with that initial view.

The authors concluded that participants established a reference direction upon first experiencing the environment, and that this organization was not updated even after learning from many other views. Second, Shelton and McNamara (2001; also see Hintzman, O'Dell & Arndt, 1981) found that the environmental shape has a profound impact on selecting reference directions. In one of their experiments, participants learned a layout of objects on the floor of a rectangular room. Learning occurred from two perspectives, one parallel with the long axis of the room and one misaligned with the room axis. Perspective taking performance was best when imagining the aligned learning perspective and performance on the misaligned learning perspective was no better than on non-experienced perspectives. The authors concluded that reference directions are selected based on a combination of egocentric experience and environmental structure, and that the rectangular room served as a cue to selecting a reference direction consistent with that structure. This finding is supported by other work showing facilitated retrieval of inter-object relationships aligned with salient environmental features like city streets, large buildings, and lakes (McNamara, Rump & Werner, 2003; Montello, 1991; Werner & Schmidt, 1999).

Other work has shown that selection of reference directions is influenced not only by features external to the learned layout, but also by the structure of the learned layout itself. For example, the reference directions used to remember the locations of cars in a stadium parking lot might be influenced by the row and column structure of the very cars that are being learned. Mou and McNamara (2002) demonstrated the influence of this intrinsic structure by having participants study a rectilinear object array. The experimenter pointed out the spatial regularity of the layout, which contained rows and columns oblique to the viewing perspective during learning. Subsequent perspective taking performance was best for perspectives aligned with the intrinsic axes defined by the rows and columns of objects, even though those perspectives were never directly experienced during learning. Furthermore, this influence of the intrinsic object structure is not dependent on experimenter instructions like those provided in Mou and McNamara's experiments. Instead, an axis of bilateral symmetry within the object array can induce the same organization with respect to an intrinsic frame of reference, defined by the symmetry axis (Mou, Zhao & McNamara, 2007).

To summarize the findings reviewed so far, the reference directions used to organize long-term spatial memories are known to be influenced by egocentric experience, extrinsic environmental structures like room walls (extrinsic to the learned layout), and intrinsic structures like rows and columns of objects or symmetry axes (intrinsic to the learned layout). While these cues have each proven influential in cases where only one or two cues are available, real world environments typically contain a whole host of cues, including numerous extrinsic and intrinsic cues like sidewalks, tree lines, waterfronts, and mountain ranges. A recent set of experiments reported by Kelly & McNamara (2008) sought to determine whether one particular cue type is dominant in a more representative scene, where egocentric experience, extrinsic structure, and intrinsic structure all provided potential cues to selecting a reference direction. In the first of two experiments using immersive virtual reality, participants learned a layout of seven virtual objects from two perspectives. The objects were arranged in rows and columns which were oblique to the walls of a surrounding square room (termed the incongruent environment, since intrinsic and extrinsic environmental structures

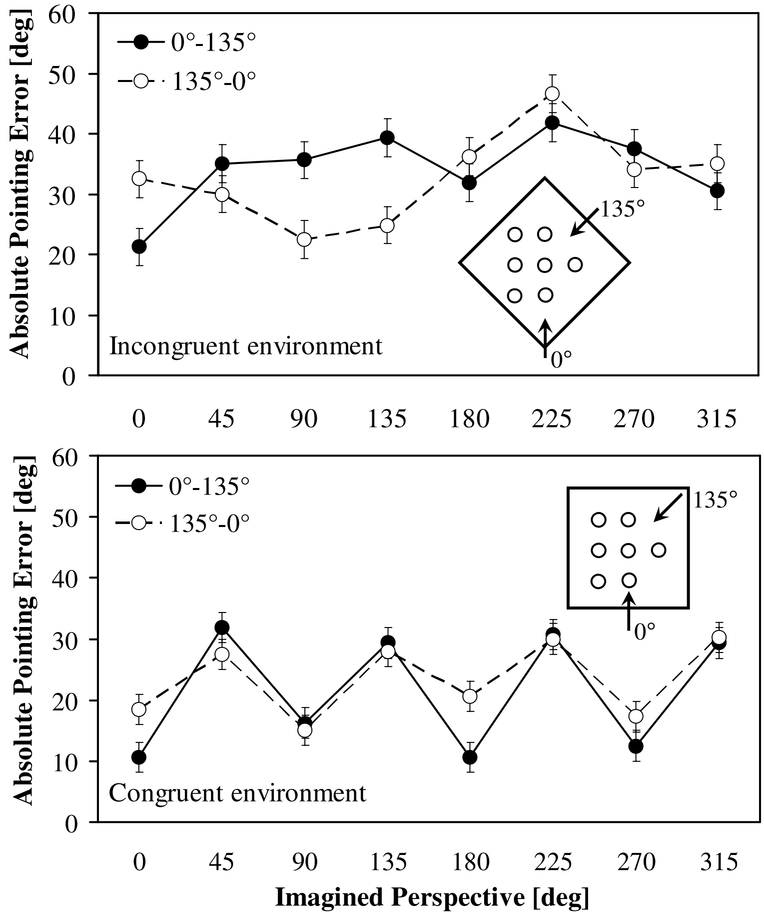

Fig. 1. Stimuli and results from Kelly and McNamara (2008). Plan views of the incongruent (top) and congruent (bottom) environments appear as insets within each panel. In the plan views, open circles represent object locations, solid lines represent room walls, and arrows represent viewing locations during learning. Pointing error is plotted as function of imagined perspective, separately for the two viewing orders (0° then 135° or 135° then 0°). After learning the incongruent environment (top), where intrinsic and extrinsic structures were incongruent with one another, performance was best on the initially experienced view. After learning the congruent environment (bottom), where intrinsic and extrinsic structures were congruent with one another, performance was best for perspectives aligned with the redundant environmental structures, regardless of viewing order.

were incongruent with one another; see Figure 1, top panel). One of the learned perspectives (0°) was aligned with the intrinsic object structure, and the other (135°) was aligned with the extrinsic room structure. Learning occurred from both views, and viewing order was manipulated. If the intrinsic structure was more salient than extrinsic structure, then participants should have selected a reference direction from the 0°

view (aligned with the rows and columns of the layout). However, if extrinsic structure was more salient than intrinsic structure, then participants should have selected a reference direction from the 135° view (aligned with the walls of the room). Finally, if the competing intrinsic and extrinsic structures negated one another's influence, then participants should have selected a reference direction from the initially experienced view, regardless of its alignment with a particular environmental structure. In fact, spatial memories of the incongruent environment (top panel of Figure 1) were based on the initially experienced view, and the pattern of facilitation is well predicted by the viewing order. Neither the intrinsic structure of the objects nor the extrinsic structure of the room was more salient when the two were placed in competition.

In the second experiment reported by Kelly and McNamara (2008), the intrinsic and extrinsic structures were placed in alignment with one another (termed the congruent environment; see inset in Figure 1, bottom panel), and learning occurred from two perspectives, one aligned and one misaligned with the congruent environmental structures. Spatial memories of the congruent environment (bottom panel of Figure 1) were organized around the redundantly defined environmental axes. Performance was best for perspectives aligned with the congruent intrinsic and extrinsic structures, and was no better on the misaligned experienced view than on other misaligned views that were never experienced. The results of these two experiments fit well with those reported by Shelton and McNamara (2001), where multiple misaligned extrinsic structures (a rectangular room and a square mat on the floor) resulted in egocentric selection of reference directions, but aligned extrinsic structures resulted in environment-based selection. Taken together, these findings indicate that intrinsic and extrinsic structures are equally salient, and can serve to reinforce or negate the influences of one another as cues to the selection of reference directions. Every-day environments typically contain multiple intrinsic and extrinsic structures like roads, waterfronts, and tree lines, and these structures often define incongruent sets of environmental axes. As such, it is possible that reference directions are most commonly selected on the basis of egocentric experience.

Experiments on long-term spatial memory have regularly provided evidence that long-term representations are orientation-dependent, allowing for privileged access to spatial relations aligned with a reference direction centered on the environment. However, the evidence reviewed thus far is based primarily on imagined perspective taking performance, and experiments using scene recognition indicate that there may be more than one long-term representation. Valiquette and McNamara (2007; also see Shelton & McNamara, 2004) had participants learn a layout of objects from two perspectives, one aligned and one misaligned with the extrinsic structure of the environment (redundantly defined by the room walls and a square mat on the floor). As in other experiments (e.g., Kelly & McNamara, 2008; Shelton & McNamara, 2001), perspective taking performance was better when imagining the aligned learning perspective than when imagining the misaligned learning perspective, which was no better than when imagining other misaligned perspectives that were never experienced. In contrast, scene recognition performance was good on both the aligned and misaligned learning perspectives, and fell off as a function of angular distance from the learned perspectives. So while imagined perspective taking performance indicated that the misaligned learning view was not represented in long-term memory, scene recognition performance indicated that the misaligned view was represented. The authors interpreted this as evidence for two long-term representations, one used for locating self-position (active during the scene recognition test) and the other for locating goal locations after establishing self-position (active during the perspective taking task). Importantly, both representations were found to be orientation-dependent, but the reference directions used to organize the two types of representations were different. The influence of these reference directions on navigation is still unclear. One possibility is that spatial relationships are more accessible when the navigator is aligned with a reference direction in long-term memory. As a result, a navigator's ability to locate and move toward a goal location might be affected by his or her orientation within the remembered space. Additionally, experiments presented in Section 4 suggest that spatial updating occurs with respect to the same reference directions used to organize spatial memories.

3 Sensorimotor Spatial Memory

Whereas long-term representations are suitable for reasoning about inter-object relationships from learned environments, they are, by themselves, insufficient for coordinating actions within the remembered environment. In order to act on our environments, we require a body-centered representation of space, rather than the environment-centered representations characteristic of long-term spatial memories. Indeed, current theories of spatial memory (e.g., Avraamides & Kelly, 2008; Kelly et al., 2007; Mou et al., 2004; Rump & McNamara, 2007; Sholl, 2001) typically include something analogous to a sensorimotor spatial memory system, which represents egocentric locations of objects in the environment and can be used to negotiate obstacles, intercept moving objects, and steer a straight course toward a goal. This sensorimotor representation provides privileged access to objects in front of the body, evidenced by the finding that retrieval of unseen object locations is facilitated for locations in front of the body, compared to behind (Sholl, 1987). This same pattern also occurs when imagining perspectives within a remote environment stored in long-term memory (Hintzman et al., 1981; Shelton & McNamara, 1997; Werner & Schmidt, 1999), where pointing from an imagined perspective is facilitated for objects in front of the imagined position, relative to objects behind, and suggests that the sensorimotor representation might also be used to access spatial relationships from non-occupied environments (Sholl, 2001). This privileged access to objects in front is consistent with other front-facing aspects of human sensory and locomotor abilities, and highlights the importance of locations and events in front of the body.

Unlike the environment-centered reference frames characteristic of long-term spatial memories, egocentric locations within the sensorimotor representation must be updated during movement through the environment. Because this updating process is cognitively demanding, there is a limit to the number of objects that can be updated successfully (Wang et al., 2006; but see Hodgson & Waller, 2006). Furthermore, self-motion cues are critical to successful updating, and a large body of work has studied the effectiveness of various self-motion cues. While updating the location of one or two objects can be done fairly effectively during physical movements, imagined movements, which lack the corresponding self-motion cues, are comparatively quite difficult (Rieser, 1989). In a seminal study on imagined movements, Rieser asked blindfolded participants to point to remembered object locations after physical rotations or after imagined rotations. Pointing was equally good before and after physical rotations, indicating the efficiency of updating in the presence of self-motion cues. However, performance degraded as a function of rotation angle after imagined rotation. According to Presson and Montello (1994; also see Presson, 1987), pointing judgments from imagined perspectives misaligned with the body are difficult because of a reference frame conflict between two competing representations of the surrounding environment. The remembered environment in relationship to one's *physical* location and orientation is held in a primary representation (i.e., the sensorimotor representation), and the same environment relative to one's *imagined* location and orientation is held in a secondary representation. Imagined movement away from one's physical location and orientation creates conflict between these two representations, referred to here as sensorimotor interference (May, 2004). This conflict occurs when the primary and secondary representations both represent the same environment, and therefore sensorimotor interference only affects perspective-taking performance when imagining perspectives within the occupied environment, but not when imaging perspectives from a remote environment.

Much of the research on the sensorimotor representation has been conducted independently from research on long-term spatial memory (reviewed above in Section 2). However, recent experiments indicate that a complete understanding of the sensorimotor representation must also take into account the organization of long-term spatial memory. Experiments by Mou et al. (2004) indicate that the interference associated with imagining a perspective misaligned with the body depends on whether that imagined perspective is aligned with a reference direction in long-term memory. They found that the sensorimotor interference associated with imagining a perspective misaligned with the body was larger when the imagined perspective was also misaligned with a reference direction in long-term memory, compared to perspectives aligned with a reference direction. However, a thorough exploration of this interaction between sensorimotor interference and reference frames in long-term spatial memory is still lacking.

As proposed by Mou et al. (2004), the sensorimotor representation is transient, and decays at retention intervals of less than 10 seconds in the absence of perceptual support. However, experiments by Kelly et al. (2007) challenge this notion based on the finding that sensorimotor interference can occur after long delays involving extensive observer movements. In one experiment using immersive virtual reality, participants learned a circular layout of objects within a room. Although participants were allowed unrestricted viewing of the virtual environment, the initially experienced view was held constant across participants. The objects were removed after learning, and subsequent spatial memory retrieval occurred over two blocks of testing. In each block, participants imagined perspectives within the learned set of objects, and those perspectives could be 1) aligned with the initially experienced view (termed the "original" perspective), 2) aligned with the participant's actual body orientation during retrieval (termed the "sensorimotor aligned" perspective), or 3) misaligned with both the initially experienced view and the participant's body orientation (termed the "misaligned" perspective). Prior to starting the first block of trials, participants walked three meters into a neighboring virtual room. Perspective taking performance when standing in this neighboring room was best when imagining the initially experienced perspective (compare performance on the original perspective with performance on the misaligned perspective in Figure 2), but there was no advantage for the perspective aligned, compared to misaligned with the body (compare performance on the sensorimotor aligned perspective with performance on the misaligned perspective). Based on results from this first test block, the authors concluded that participants' sensorimotor representations of the learned objects were purged upon leaving the learning room and replaced with new sensorimotor representations of the currently occupied environment (i.e., the room adjacent to the learning room). As such, there was no sensorimotor interference when imagining the learned layout while standing in the neighboring room. Using Presson and Montello's (1994) framework, participants' primary and secondary spatial representations contained spatial information from separate environments, and therefore no sensorimotor interference occurred.

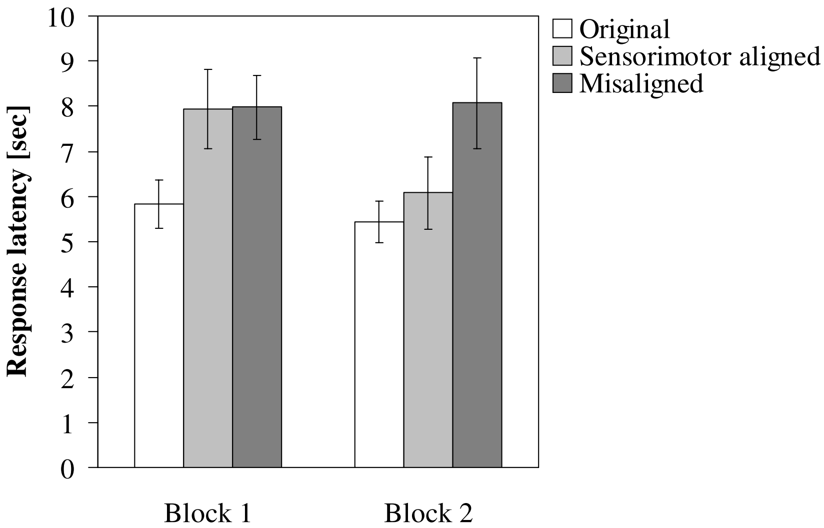

Fig. 2. Results of Kelly, Avraamides and Loomis (2007). Response latency is plotted as a function of test block and imagined perspective. After learning a layout of objects, participants walked into a neighboring room and performed Block 1 of the perspective-taking task. Results indicate that performance was best for the originally experienced perspective during learning, but was unaffected by the disparity between the orientation of the imagined perspective relative to the orientation of the participants' bodies during testing. After completing Block 1, participants returned to the empty learning room and performed Block 2. Results indicate that performance was facilitated on the originally experienced perspective, and also on the perspective aligned with the body during testing.

For the second block of trials, participants returned to the empty learning room (the learned objects had been removed after learning), and performed the exact same perspective-taking task as before. Performance was again facilitated when participants imagined the initially experienced perspective, but also when they imagined their actual perspective, compared to performance on the misaligned perspective (see Figure 2). Despite the fact that participants did not view the learned objects upon returning to the learning room, their sensorimotor representations of the objects were reactivated, causing sensorimotor interference when imagining perspectives misaligned with the body. This indicates that walking back into the empty learning room was sufficient to reinstantiate the sensorimotor representation of the learned objects, even though several minutes had passed since they were last seen. Renewal of the sensorimotor representation must have drawn on the long-term representation, because the objects themselves were not experienced upon returning to the empty learning room. In sum, Kelly et al.'s experiment suggests that the sensorimotor representation is less sensitive to elapsed time than previously thought, and instead is dependent on perceived self-location. The sensorimotor representation appears to be context dependent, and moving from one room to another changes the context and therefore also changes the contents of the sensorimotor representation.

4 Spatial Orientation

Staying oriented during movement through a remembered space and reorienting after becoming lost are critical spatial abilities. With maps and GPS systems, getting lost on one's drive home might not present a life or death situation, but the same was not true for our ancestors, whose navigation abilities were necessary for survival. According to Gallistel (1980; 1990), spatial orientation is achieved, in part, by relating properties of the perceived environment (i.e., the sensorimotor representation) with those same properties in the remembered environment (i.e., the long-term representation), and is also informed by perceived self-position as estimated by integrating self-motion cues during locomotion, a process known as path integration. The importance of information from path integration becomes particularly clear when navigating within an ambiguous environment, such as an empty rectangular room in which two orientations provide the exact same perspective of the room (e.g., Hermer & Spelke, 1994). In this case, one's true orientation can only be known by using path integration to distinguish between the two potentially correct matches between sensorimotor and long-term representations.

From time to time, the matching between perceived and remembered environments can produce grossly incorrect estimates of self-position. Jonsson (2002; also see Gallistel, 1980) describes several such experiences. In one case, he describes arriving in Cologne by train. Because his origin of travel was west of Cologne, he assumed that the train was facing eastward upon its arrival at Cologne Central Station. The train had, in fact, traveled past Cologne and turned around to enter the station from the east, and was therefore facing westward upon its arrival. Jonsson's initial explorations of the city quickly revealed his orienting error, and he describes the disorienting experience of rotating his mental representation of the city 180° into alignment with the visible scene. Experiences such as these are typically preceded by some activity that disrupts the path integration system (like riding in a subway, or falling asleep on a train), which would have normally prevented such an enormous error.

4.1 Environmental Cues to Spatial Orientation

Much of the experimental work on the topic of human spatial orientation has focused on the cues used to reorient after explicit disorientation. In particular, those studies distinguish between two types of environmental cues to spatial orientation: 1) geometric cues, such as the shape of the room as defined by its extended surfaces, and 2) featural cues, such as colors, textures, and other salient features that cannot be described in purely geometric terms (see Cheng & Newcombe, 2005, for an overview of the findings in this area). The majority of these experiments employ a task originally developed by Cheng (1986) to study spatial orientation in rats. Hermer and Spelke (1994, 1996) adapted Cheng's task to study reorientation in humans. In the basic experimental paradigm, participants learn to locate one corner within a rectangular room, consisting of two long walls and two short walls. Participants are later blindfolded and disoriented, and are then asked to identify which corner is the learned corner. When all four room walls are uniformly colored (Hermer & Spelke, 1996), participants split their responses evenly between the correct corner and the diagonally opposite corner, both of which share the same ratio of left and right wall lengths and the same corner angle. Rarely do participants choose one of the geometrically incorrect corners, a testament to their sensitivity to environmental geometry and their ability to reorient using geometric cues. When a featural cue is added by painting one of the four walls a unique color (Hermer & Spelke, 1996), participants are able to consistently identify the correct corner and no longer choose the diagonally opposite corner, indicating the influence of featural cues on reorientation.

Recent experiments in our lab have focused on room rotational symmetry as the underlying geometric cue in determining reorientation performance. Rotational symmetry is defined as the number of possible orientations of the environment that result in the exact same perspective. For example, any perspective within a rectangular

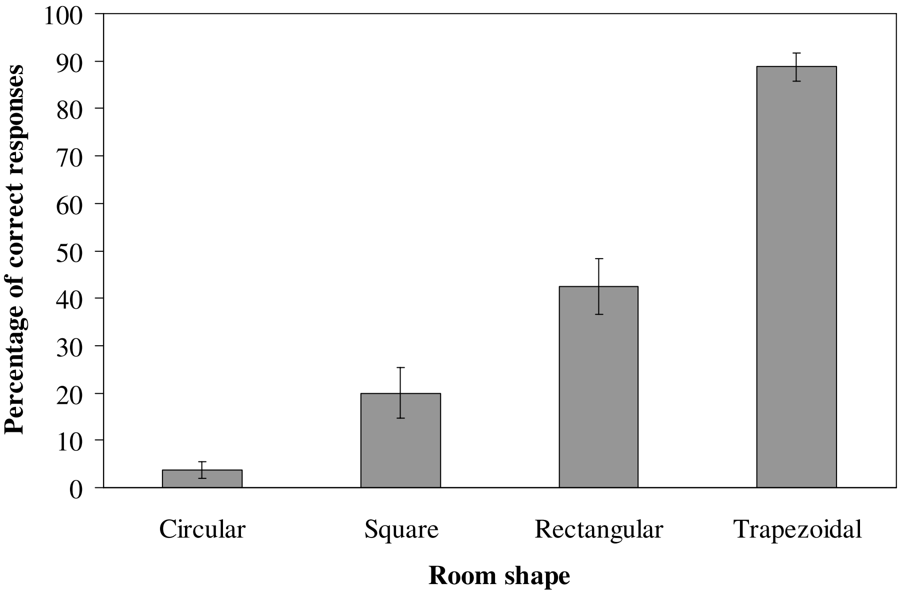

Fig. 3. Reorientation performance in four rooms, varying in their rotational symmetry. Participants learned to identify one of twelve possible object locations, and then attempted to locate the learned location after disorientation.

room (without featural cues) can be exactly reproduced by rotating the room 180°. Because there are two orientations that produce the same perspective, the rectangular room is two-fold rotationally symmetric. A square room is four-fold rotationally symmetric, and so on. In our experiment, we tested reorientation performance within environments of 1-fold (trapezoidal), 2-fold (rectangular), 4-fold (square) and ∞-fold (circular) rotational symmetry. Participants memorized one of twelve possible target locations within the room, and then attempted to re-locate the target position after explicit disorientation. Reorientation performance (see Figure 3) was inversely proportional to room rotational symmetry across the range of rotational symmetries tested. This can be considered an effect of geometric ambiguity, with the greater ambiguity of the square room compared to the trapezoidal room leading to comparatively poorer reorientation performance in the square room. The same analysis can be applied to featural cues, which have traditionally been operationalized as unambiguous indicators of self-location (e.g., Hermer & Spelke, 1996), but need not be unambiguous.

4.2 Path Integration

Even in the absence of environmental cues, humans can maintain a sense of spatial orientation through path integration. Path integration is the process of updating perceived self-location and orientation using internal motion cues such as vestibular and proprioceptive cues, and external motion cues such as optic flow, and integrating those motion signals over time to estimate self-location and orientation (for a review, see Loomis, Klatzky, Golledge & Philbeck, 1999).

The path integration process is noisy, and errors accrue with increased walking and turning. In an experiment by Klatzky et al. (1990), blindfolded participants were led along an outbound path consisting of one to three path segments, and each segment was separated by a turn. After reaching the end of the path, participants were first asked to turn and face the path origin and then to walk to the location of the path origin. Turning errors and walked-distance errors increased with the number of path segments, demonstrating that path integration is subject to noise. Errors that accumulate during path integration cannot be corrected for without perceptual access to environmental features, such as landmarks or geometry.

4.3 Spatial Orientation Using Path Integration and Environmental Cues

Only occasionally are we faced with a pure reorientation task or a pure path integration task. More commonly, environmental cues and path integration are both available as we travel through a remembered space. In a recent experiment, we investigated the role of environmental geometry in spatial orientation when path integration was also available. Participants performed a spatial updating task, where they learned a location within a room and attempted to keep track of that location while walking along an outbound path. At the end of the path they were asked to point to the remembered location. The path was defined by the experimenter and varied in length from two to six path segments, and participants actively guided themselves along this path. The task was performed in environments of 1-fold (trapezoidal), 2-fold (rectangular), 4-fold (square) and ∞-fold (circular) rotational symmetry. If rotational symmetry affects spatial updating performance like it affected reorientation performance (see Section 4.1, above), then performance should degrade as room shape becomes progressively more ambiguous. The effect of room rotational symmetry was expected to be particularly noticeable at long path lengths, when self-position estimates through path integration become especially error-prone (Klatzky et al., 1990; Rieser & Rider, 1991), and people are likely to become lost and require reorientation. Contrary to these predictions, spatial updating performance was quite good, and was unaffected by increasing path length in all three angled environments (square, rectangular and trapezoidal; see Figure 4). This is in stark contrast to performance in the circular room, where errors increased with increasing path length. Participants were certainly using path integration to stay oriented when performing the task. Otherwise, performance would have been completely predicted by room rotational symmetry (like the reorientation experiment discussed above in Section 4.1). Participants were also certainly using room shape cues, when available. Otherwise, pointing errors in all environments would have increased with increasing path length, as they did in the circular room.

To explain these results, we draw on previous work showing that long-term spatial memories are represented with respect to a small number of reference directions (see Section 2). Of particular relevance, Mou et al. (2007) showed that reference directions often correspond to an axis of environmental symmetry. Based on this finding, we believe that participants in the spatial updating task represented each environment (including the room itself and the to-be-remembered locations within the room) with respect to a reference direction, coincident with an environmental symmetry axis. Perceived self-position was updated with respect to this reference direction (see Cheng & Gallistel, 2005, for a similar interpretation of experiments on reorientation by rats). In the circular room, any error in estimating self-position relative to the reference direction directly resulted in pointing error, because the environment itself offered no information to help participants constrain their estimates of the orientation of the reference direction. However, geometric cues in the three angled environments at least partially defined the reference direction, which we believe corresponded to an environmental symmetry axis. For example, the square environment defined the symmetry axis within +/- 45°. If errors in perceived heading ever exceeded this +/- 45° threshold, then participants would have mistaken a neighboring symmetry axis for the selected reference direction. The rectangular and trapezoidal environments were even more forgiving, as the environmental geometries defined those symmetry axes within +/- 90° and +/- 180°, respectively. Furthermore, participants in the angled environments could use the environmental geometry to reduce heading errors during locomotion, thereby preventing those errors from exceeding the threshold allowed by a given rotational symmetry.

The experiments described in this section demonstrate how ambiguous environmental cues and noisy self-motion cues can be combined to allow for successful spatial orientation. During normal navigation, we typically have information from multiple sources, all of which may be imperfect indicators of self-position. By combining those information sources, we can stay oriented with respect to the remembered environment, a crucial step toward successful navigation.

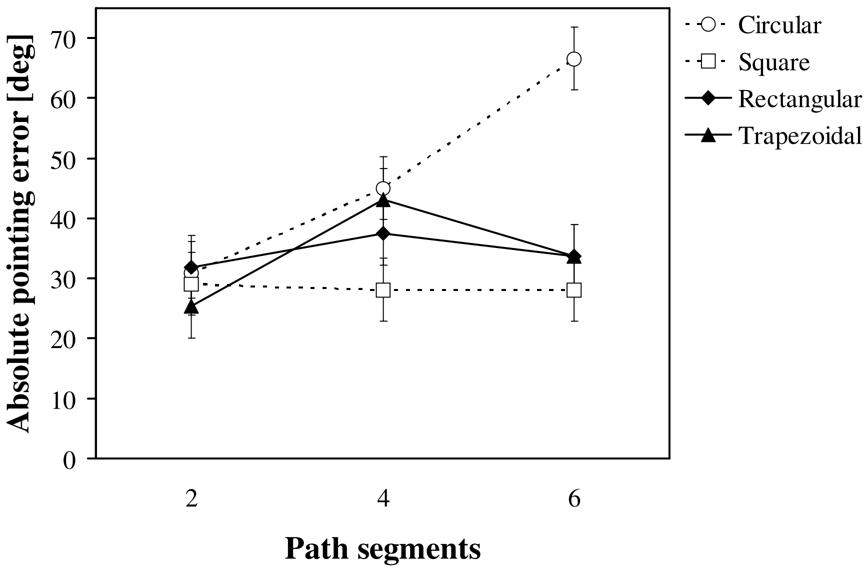

Fig. 4. Pointing error in a spatial updating task as a function of walked path length, plotted separately for the four different surrounding environments. Pointing errors increased with increased walking distance in the round room. In comparison, performance was unaffected by path length in the square, rectangular, and trapezoidal rooms.

5 Summary and Conclusions

Although sensorimotor and long-term spatial memories have traditionally been researched separately, the current overview indicates that a complete description of navigation will depend on a better understanding of how these spatial representations are coordinated to achieve an accurate sense of spatial orientation. This chapter has reviewed the evidence that long-term spatial memories are orientation-dependent, and that the selection of reference directions depends on egocentric experiences within the environment as well as environmentally defined structures, such as intrinsic and extrinsic axes. Environmental symmetry axes are particularly salient cues shown to influence reference frame selection (Mou et al., 2007). Furthermore, the sensorimotor representation can access this long-term representation under certain circumstances. In the experiment by Kelly et al. (2007), the sensorimotor representation of objects from a previously experienced environment could be reified even though participants never actually viewed the represented objects again. The environmental context allowed participants to retrieve object locations from long-term memory and rebuild their sensorimotor representations of those retrieved objects. Building up the sensorimotor representation through retrieval of information stored in long-term memory is necessary when navigating toward unseen goal locations. Furthermore, the sensorimotor representation is likely to be partially responsible for generating and adding to the long-term representation. By keeping track of one's movements through a new environment, new objects contained in the sensorimotor representation (i.e., novel objects in the visual field) can be added to the long-term, environment-centered spatial memory. However, the nature of these interactions between long-term and sensorimotor spatial memories remains poorly understood, and warrants further research.

The experiments on spatial orientation presented in Section 4 represent a step toward understanding this interaction between sensorimotor and long-term representations. Participants in those experiments are believed to have monitored self-position and orientation relative to the reference direction used to structure the long-term memory of the environment, and the selected reference direction most likely corresponded to an axis of environmental symmetry. Path integration helped participants keep track of the selected reference direction and avoid confusion with neighboring symmetry axes. This conclusion underscores the importance of the reference directions used in long-term memory, not just for retrieving inter-object relationships, but also for staying oriented within remembered spaces and updating those spaces during self-motion. A more complete understanding of spatial orientation should be informed by further studies of the interaction between long-term spatial memory, sensorimotor spatial memory, and path integration.

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